A Contribution to the Biology of the Convict Surgeonfish of the Hawaiian Islands, *Acanthurus triostegus sandvicensis*[1]

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THE SURGEONFISHES (family Acanthuridae), which are distinctive chiefly in their possession of a knifelike spine or spines at the base of the tail, are one of the dominant groups of tropical inshore marine fishes. Over much of their vast range, including Hawaii, where they are especially prominent on the reefs, they are important components of subsistence fisheries. Little is known of their biology, however. There are only scattered references to the herbivorous food habits of the group and general remarks on the habitat of certain species.

An analysis of the generic classification of the family and taxonomic revisions of some of the genera have been published (Randall, 1955 *a*, *c*, *d*; 1956*b*). The largest genus, *Acanthurus*, contains 32 species, 4 of which occur in the Atlantic, and the rest in the Indo-Pacific. The present paper constitutes a report of a study made during 1952–55 upon the life history and the ecology of one Hawaiian subspecies of this genus, *A. triostegus sandvicensis*, the convict tang or convict surgeonfish. In Hawaii and elsewhere in Polynesia this surgeonfish is known as the manini, and hereafter it will usually be referred to by that name.

The manini is the most abundant species of surgeonfish in the Hawaiian Islands and commercially the most important. Judging from its prevalence in museum collections, it is also common elsewhere in the Indo-Pacific region. Jordan and Seale (1906: 354) wrote, "This species is the most abundant of the genus about Samoa, swarming everywhere on the reefs." The young reside in tidepools, and are therefore more accessible for observation and experimentation than the young of other acanthurids in Hawaii which are usually found in deeper water. The species has the widest distribution of all of the surgeonfishes—East Africa to the Gulf of California (a single record from West Africa by Fowler, 1936, should be confirmed). Thus interest in its biology may be greater than that of a localized species.

A. triostegus (Fig. 1) has been described under 10 different scientific names and placed in six different genera. Nomenclatural considerations and description of the species and variants, with special reference to fin-ray counts and coloration, have been dealt with previously (Randall, 1956*b*).

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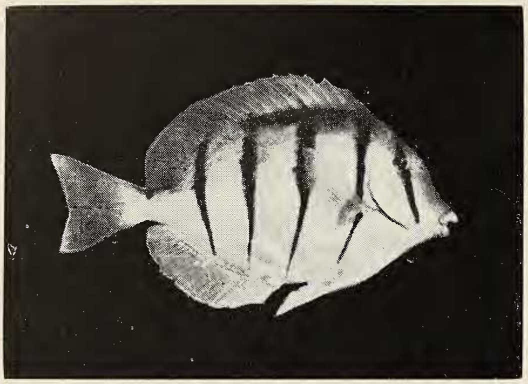


FIG. 1. Adult manini, *Acanthurus triostegus sandvicensis,* from Hawaii. Standard length, 154 mm.

HABITAT

In the Hawaiian Islands the manini occupies a diversity of habitats. It occurs in bays, harbors, and exposed reef areas. It abounds in tide pools and shallow water, yet is known at depths of at least 100 ft. Areas of very turbid and brackish water are usually avoided, but a few manini have been collected even in these regions.

Like most reef fishes, the manini avoids extensive stretches of sand or mud bottom, preferring instead the nearness of holes or crevices in the reef for shelter and solid bottom for the growth of its algal food.

The manini appears to be more restricted in habitat in the Gilbert and Marshall islands, possibly because of the sharper definition of the ecological zones of these atolls. It occurs in these atolls both in the lagoon and outer reef areas; however it seems to be confined to relatively shallow water. On the outer reef the fish were seen only on the reef flat, the young in great abundance in the shallower sections and the adults on the seaward portions (for data from a reef-flat transect in the Gilbert Islands, see Randall, 1955*b*: 181). The species was only rarely observed in the turbulent surge channel zone and was never seen on the coralliferous terrace (benched area of living coral offshore from the reef flat).

As in the Gilberts and Marshalls, the presence of heavy coralline areas in the Hawaiian Islands seems to limit the manini. This is apparent from the underwater transect work of Brock (1954). Areas like the northern part of Kealakekua Bay, Hawaii, where the coral growth is extremely rich for the Hawaiian region, are almost devoid of manini. Since this species is herbivorous, its diminution in coral areas may be associated with the small amount of substratum available for the growth of algae. Surprisingly, other surgeonfishes such as *Acanthurus leucopareius*, *A. achilles*, *Zebrasoma flavescens*, and *Ctenochaetus strigosus*, usually less abundant than manini, are the most common fishes in this part of the bay. With the exception of *C. strigosus* which is a detritus feeder (Randall, 1955*d*), these species are more inclined to crop close to the substratum than the manini, judging from the greater amount of inorganic debris in their stomach contents, and they may therefore be superior competitors under such conditions.

The eggs and larvae of the manini are pelagic. This has been ascertained by a study of development following artificial fertilization of the eggs, by the capture of larvae in plankton nets, and by the taking of the late postlarval or acronurus stage at night lights offshore.

A total of 11 acanthurid larvae (at least 3 of which are manini), 4.2–8.7 mm. in total length, were found in the plankton collections from Hawaiian waters of Cruises 4 (May 1950) and 6 (August 1950) of the "Hugh M. Smith," a POFI research vessel. These fish were taken at eight stations ranging from about 10 to 140 mi. from the nearest island (for more exact locations, see King and Hida, 1954: fig. 1, stations 1A, 10, 13, 15, 17, and 23 of Cruise 4 and stations 7 and 14 of Cruise 6). They were captured in horizontal tows made with fine-meshed plankton nets (1 m.) which sampled three different levels simultaneously. For both cruises combined, a total of 58 hauls were made at the surface, 24 at a depth of 50 m., and 112 at depths from 100 to 300 m. Six of the larvae were taken at the surface, 5 at 50 m., and none at greater depths. The failure to find more larvae in these collections is probably due to the distance from land of most of the stations. Only 6 of the 29 stations of each cruise were within 25 mi. of any of the Hawaiian Islands and only 1 within 10 mi. The absence of larval *Acanthurus* longer than 8.7 mm. in the collections is probably due to the ability of larger larvae to elude the plankton net. The lack of specimens shorter than 4.2 mm. may be the result of a paucity of small larvae so far offshore.

That acanthurid larvae, in general, are more abundant close to land has been shown by Reintjes and King (1953). These authors found a total of 1,067 acanthurid larvae in the stomach of 184 of 1,097 yellowfin tuna (*Thunnus macropterus*) sampled from the region of the Line and Phoenix islands. They stated that the acanthurids were common in the stomachs of nearshore yellowfin, along with balistids and carangids. Representatives of the Bramidae, Exocoetidae, and Gempylidae predominated in the stomachs of offshore yellowfin.

King kindly allowed me to examine the stomach content work sheets in order to compare the occurrence of larval acanthurids in the stomachs of tuna caught at the surface by pole-and-line fishing and by trolling with those caught at depths of about 30 to 160 mi. by long-lining. The comparison revealed more acanthurid larvae in the stomachs of surface-caught fish.

The acronurus larval form of the manini, averaging about 26 mm. in standard length in the Hawaiian Islands, leaves the pelagic realm and enters very shallow water, often tide pools, to transform to the juvenile stage. Although juveniles tend to remain in shallow water, there is a progressive movement with increasing size to somewhat deeper water. Adults are not entirely absent from tide pools, however. Several were seen in pools 1–3 ft. deep cut off from the open sea at low tide on Moku Manu and Manana (Rabbit) islands. Also, at night on Oahu, manini as large as 70 mm. were occasionally found in high tide pools.

TOLERANCE TO TEMPERATURE AND SALINITY

In order to determine if the manini is capable of surviving the extremes of temperatures and salinity which it encounters on Oahu, a survey of these factors in tide pools and brackish areas known to be penetrated by the species was undertaken and compared with the tolerance of the species to these factors as determined by laboratory experiments on both juveniles and adults.

Environmental Extremes

The survey of environmental temperature and salinity was not made on any regular schedule. Only when conditions occurred which suggested that high and low values of temperature and salinity might be found, were measurements of these factors made. Temperatures were taken at mid-depth of the tide pools tested. Water samples from which chlorinity was determined were obtained after stirring the pools. The Mohr method was used to determine chlorinity, and the results are expressed as grams of chlorine per kilogram of sea water (‰).

The maximum temperature, 35.1° C., was recorded in a tide pool with basalt bottom (almost black) at Makapuu Point on August 31, 1953, at 2:00 P.M. A reverse stratification of temperature existed in the pool at that time. A +0.2 low tide had occurred at 1:50 P.M. The maximum air temperature at Makapuu Point for August 31 was 79° F. (26.2° C.). Other fishes observed in the tide pool along with manini included aholehole (*Kuhlia sandvicensis*) and kupipi (*Abudefduf sordidus*).

The minimum temperature, 16.2° C., was recorded in a small tide pool at Diamond Head on March 5, 1954, at 11:15 P.M. A –0.2 low tide had occurred at Honolulu at 10:42 P.M. The minimum air temperature during the night was 60° F. (15.5° C.). A strong northerly wind was blowing. The wind velocity for the hour prior to the temperature reading was as high as 33 knots.

The extremes of environmental temperature recorded by Tester and Takata (1953: 48) for the aholehole on Oahu are 20.1° C. and 32.1° C. Like the manini, young aholehole are tide-pool residents. Although found in the highest pools of the intertidal zone, they are less inclined than the manini to enter small pools. A more notable difference of these two species is the ability of the aholehole to live in streams with little or no salt content.

The lowest chlorinity recorded from pools where manini were observed was 2.65 ‰. This reading was obtained from a high tide pool at Diamond Head during a heavy rain at 9:00 A.M. on March 1, 1954. A +0.1 low tide occurred at 9:02 A.M. A rivulet of rain water was observed entering the pool.

Another low chlorinity (3.62 ‰) was obtained in a sample taken from the shore of the Ala Wai Canal at the Ala Moana Bridge on February 23, 1954, following a heavy rain. Although manini could not be seen at the time because of the turbidity of the water, they were observed in the area prior to the rain and after the water had cleared.

The highest chlorinity was 21.30 ‰. The water sample was taken from the pool at Makapuu Point in which the 35.1° C. temperature was recorded.

Experiments on Temperature Tolerance

The experiments on temperature tolerance were performed on manini which were maintained in aquaria at a near-constant temperature of 24° C. for at least 24 hr. The fish were placed singly in a gallon jar of sea water at the temperature of the aquarium from which they were taken. The jar was then lowered into a water-filled copper compartment containing either a heating unit or a refrigerating unit and brought to the test temperature in 1 hr. ± 10 min. The fish were kept at this temperature for 1 hr. If death ensued before the end of this hour, the time was recorded. The duration of the test period was chosen as a rough approximation of the temporal conditions of exposure to temperature extremes experienced by manini in high tide pools. Throughout the tests the jar was strongly aerated.

At about 5° C. before the maximum or minimum temperatures were reached, the fish began to increase their rate of swimming and darted around the jar. As the lethal temperature was approached more closely, the equilibrium of the fish was affected. They swam on one side, upside down, or in small circles. The last major activity was usually a rapid, spasmodic, swimming movement, often in a short spiral.

The results, except those of tests of both juveniles and adults run at temperatures of 36.5° C. or less and 13° C. or greater (which caused no deaths), are shown in Table 1.

Although the data are not adequate to determine individual variation in the region of the temperature extremes, it seems evident that a range of about 13° to 36° C. is withstood by this species in the Hawaiian Islands, disregarding the possible extension of this range by acclimatization.

TABLE 1

TEMPERATURE TOLERANCE OF *Acanthurus triostegus sandvicensis*

STANDARD LENGTH (mm.)	TEST TEMP. (° C.)	MINUTES TEST TEMP. ENDURED
96	37.0	45
97	37.0	60
137	37.5	25
96	37.6	10
86	38.0	4
97	38.0	15
101	38.2	6
103	38.3	20
26	36.8	40
27	37.2	60
28	37.5	60
34	37.6	15
29	37.8	60
28	38.0	60
29	38.0	18
28	38.1	2
103	13.3	60
95	12.2	60
140	10.1	10
122	9.0	2
25	13.6	2
27	12.8	10
27	12.5	60
28	11.6	5
27	11.0	60
32	10.8	8

Although the range of temperature which manini can withstand appears to be extralimital to the extremes normally encountered by the species in the Hawaiian Islands, information supplied by D. W. Strasburg in a letter suggests that juvenile manini in the southern Marshall Islands are, upon occasions, killed in tide pools by heat. On August 17, 1950, a high tide pool, about 30 sq. ft. in surface area and 1 ft. deep, on the ocean side of Arno Atoll was observed at low tide to contain two small *Acanthurus triostegus triostegus* and one small *Istiblennius edentulus*. Several hours later the two manini were dead. The blenny was still living. The temperature of the pool at mid-depth was 41° C.

Experiments on Salinity Tolerance

Salinity tolerance experiments on manini were carried out in a 30 gal. aquarium. All fish were retained in aquaria at least 24 hr. before use in experiments. The fish were not exposed to the test salinity suddenly. Instead the salinity was gradually changed over a period of 2 hr. either by the removal of aquarium water and replacement with tap water (previously allowed to stand for at least 12 hr.) or the addition of salt from evaporated sea water. Fish were held at the test salinity for a maximum of 24 hr. The long period of exposure to salinity extremes was chosen because manini entering brackish areas may be subjected to water of low salt content for at least this length of time.

The results are given in Table 2. Omitted are trials run at chlorinity values greater than 1.4‰, none of which caused any deaths. No trials were run at chlorinities greater than 38.25 ‰.

Although more data are needed to determine with accuracy the minimum salinity which manini can withstand, it seems evident that manini in tide pools can tolerate a greater range in salinity than they normally experience. Since they cannot live in water of extremely low salinity, they probably do not enter fresh-water habitats.

PREDATORS

Predation on the manini is probably most acute during the early stages of the life history, but I have no information on the identity of the many pelagic animals that must feed on the eggs and small larvae. The large number of post-larval stages of acanthurids found in the stomachs of adult yellowfin tuna has been discussed.

Only a few instances of predation on juvenile manini have been encountered incidentally and are presented here briefly. Juvenile manini have been found in the stomachs of moray eels (Muraenidae). A small lizard fish (Synodidae) was observed to catch a juvenile manini in its jaws in shallow water in Kaneohe Bay, Oahu. The manini was too large to be swallowed, and it eventually escaped. A 50 mm. specimen of *Antennarius* was placed in an aquarium with six juvenile manini. A half hour later it had eaten one of them (length, 31 mm.).

In the Society Islands a juvenile *Caranx melampygus* about 90 mm. long was observed from shore to capture a small *Acanthurus triostegus triostegus* 25–30 mm. in length. This carangid occurs in the Hawaiian Islands where it probably feeds in part on manini, as may other species of *Caranx.*

Also in the Society Islands, the young *Acanthurus triostegus triostegus* have been found in the stomachs of the groupers *Epinephelus merra* and *Cephalopholis argus* and the snapper *Lutjanus vaigiensis* (Randall and Brock, 1960).

It is believed that predation (man excluded) on the juvenile stage of the manini in the Hawaiian Islands is much more pronounced than on the adult stage. In addition to the fishes mentioned above, holocentrids, scorpaenids, cirrhitids, and sphyraenids, and possibly also certain

TABLE 2

SALINITY TOLERANCE OF *Acanthurus triostegus sandvicensis*

NO. OF FISH	STANDARD LENGTH (mm.)	CHLORINITY (0/00)	NO. SURVIVING 24 HR.	MAXIMUM HR. SURVIVED
3	26–29	1.4	3	
4	26–29	0.7	0	5
3	27–29	0.1	0	less than 5
1	92	1.4	1	
1	89	0.7	0	8
2	86–90	0.4	0	between 3 and 15
3	27–29	34.8	2	
4	26–28	35.7	2	
3	28–29	37.4	2	
4	26–29	38.25	0	5
1	83	38.25	0	17.5

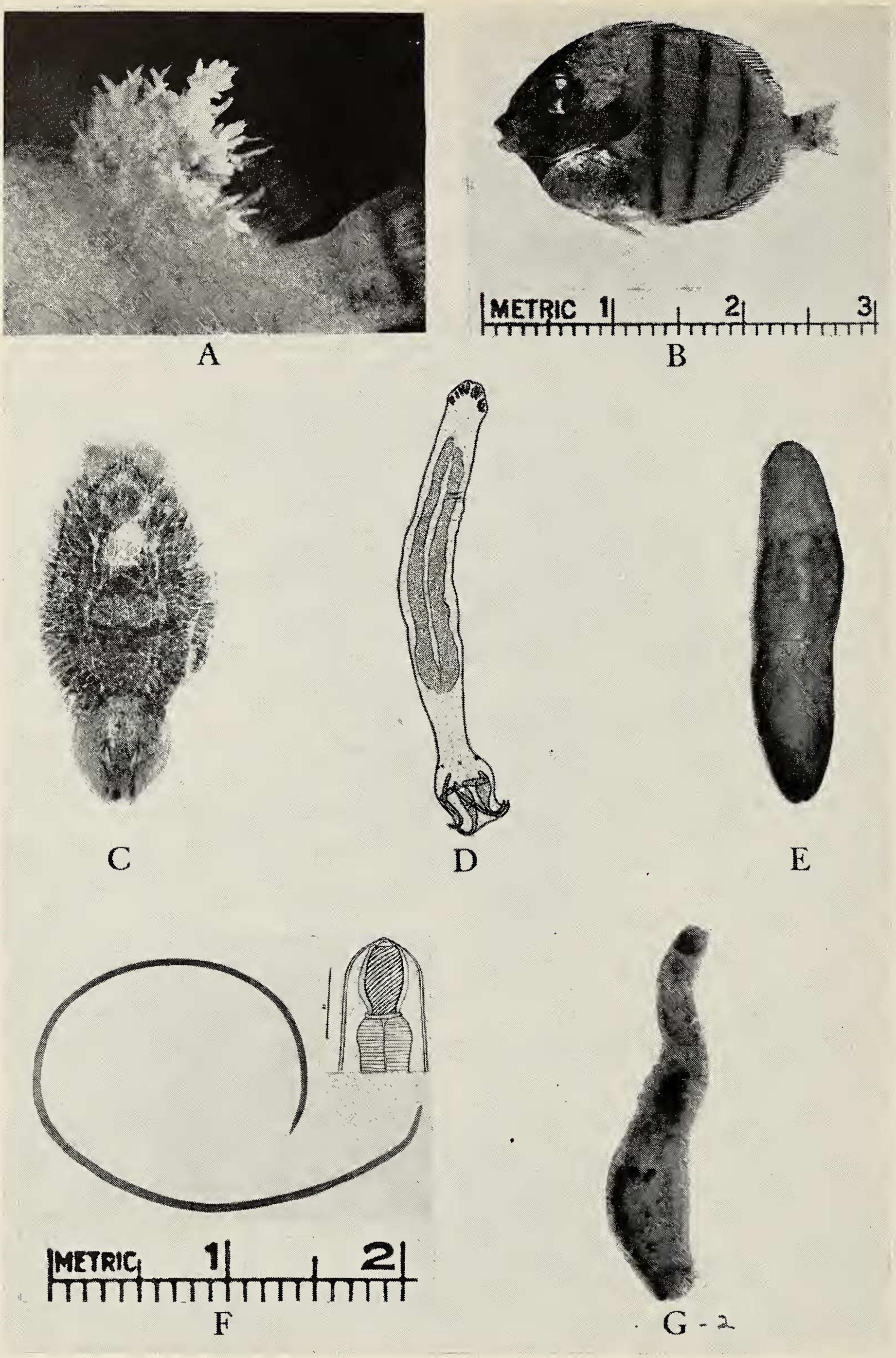


FIG. 2. Parasites of *Acanthurus triostegus sandvicensis*. *A*, Colony of *Hydrichthys* sp. on the dorsal fin of a manini in its first day of transformation from the acronurus to the juvenile state. *B*, *Hydrichthys* on the post-orbital part of the head of a manini in its second day of transformation. *C*, *Benedenia* sp. from the epidermis of an adult manini; length of trematode, 1.9 mm. *D*, *Ancyrocephalus* sp. from the gills of manini; length of trematode, 0.63 mm. *E*, *Hapladena varia* Linton from the duodenum of an adult manini; length of trematode, 2.9 mm. *F*, Adult female *Spirocamallanus monotaxis* Olsen from the intestine of adult manini; insert shows anterior end of the nematode (after Olsen, 1952); red in life, the females attain a length of about 45 mm. and the males about half this size. *G*, Unidentified leech (possibly *Johanssonia* sp.) from the gills of a manini; length of leech, 2.4 mm.

of the larger nocturnal crabs, may feed on small manini. Once a manini reaches adult size, it probably enjoys freedom from predation by most of these fishes in Hawaii, for the inshore marine fauna is peculiar in the paucity of moderately large carnivorous fishes. Shallow-water serranids and lutjanids, many of which are well adapted to prey on reef fishes, were almost totally lacking in the Hawaiian Islands until the recent effort to introduce some of these fishes. The larger native predaceous fishes, such as adults of *Caranx*, *Sphyraena*, and sharks, are not numerous at the present time, probably because of fishing pressure.

PARASITES

Seventeen species of parasites were detected on and within the manini.

Seven specimens of transforming manini were found to be parasitized by *Hydrichthys* (Fig. 2*A*), probably *H. mirus* Fewkes. This unusual hydroid occurred on the head, body, and fins and apparently does not have a preferred attachment site. It was never seen on juveniles or adults. Probably it flourishes only on postlarval manini, for it appears to be abraded and regressing on most of the transforming fish (Fig. 2*B*).

Three specimens of a monogenetic fluke (*Benedenia* sp.) were discovered on the epidermis of two adult manini. The flukes are small (less than 2 mm. in length), perfectly transparent in life, and were hidden in the slime of the fish. They are difficult to find and are probably more common than the few specimens would indicate. Figure 2*C* is a photograph of a stained specimen. Jahn and Kuhn (1932) have worked out the life cycle of *Benedenia melleni*.

The most common fluke of the manini is an unidentified species of the gyrodactylid genus *Ancyrocephalus*. Figure 2*D* is a drawing of a living specimen, 631 micra in length, which was obtained from the gills of a 132 mm. manini. This very small species of trematode was found on the gills of most of the manini which were examined. In some of the manini the infestations were heavy, an average of about one fluke per gill filament being present. It is extremely active and highly extensible and was observed to change its position on a gill filament by attaching with the anterior end and looping the posterior end over to another location where the hooks were dug into place. Siwak (1931) reported on the life cycle of a species of *Ancyrocephalus*.

Two digenetic trematodes were found in the digestive tract of the manini, *Hapladena varia* Linton and *Haplosplanchnus obtusus* (Linton), previously known only from the surgeonfishes *Acanthurus hepatus* (= *chirurgus*) and *Acanthurus coeruleus* at Tortugas, Florida. Manter (1955: 76) included a discussion of this distribution in a recent paper reviewing the zoogeography of trematodes of marine fishes.

Hapladena varia (Fig. 2*E*) was only occasionally found in the intestine of the manini. A total of 22 specimens, usually less than 3 mm. in length, were taken from 200 manini whose digestive tracts were examined for parasites. The manini harboring the flukes ranged from 43 to 136 mm. in standard length.

Haplosplanchnus obtusus was found only in juvenile manini, although it may have been overlooked in adults. It is smaller than *Hapladena varia*, usually less than 1.3 mm., and not as slender. Some of the juvenile manini contained a large number of these flukes. Seventy-one were counted in one 49 mm. specimen. Most of the flukes were in the duodenum, a few extended as far back as the halfway point of the intestine, and a few were found in the pyloric caeca.

Four different nematodes were found in the manini. Two could not be identified to genus. One of these was a very attenuate immature male from suprapharyngeal tissue of the fish. The other was represented only by larval specimens from the pyloric caeca. A third worm, which was occasionally found encysted in the mesenteries, was considered to be the immature female of an unidentified species of *Contracaecum*.

The fourth nematode, *Spirocamallanus monotaxis* (Fig. 2*F*), was described by Olsen (1952) from the sparid fish *Monotaxis grandoculis*, reportedly a mollusk-feeder. In all probability this roundworm will be found in other Hawaiian fishes.

Of 200 manini (mostly adults) from Oahu examined throughout the year for internal parasites, 76 were found which harbored *S. monotaxis* in the intestine or pyloric caeca. The average number of worms found in these 76 fishes was 5. The largest number of worms in a single fish was 35. No obvious variation of the degree of infestation of this nematode in the manini was observed during the year.

Two different leeches were found on the manini. Both are species in the family of Pisicolidae (possibly genus *Johanssonia*). One is represented by a single 2.4 mm. immature specimen (stained and photographed herein as Fig. 2*G*) which was taken from the gills of an adult manini. Six specimens of the other leech were collected from the body surface of three juvenile manini, 26–31 mm. in standard length, taken in the Ala Wai Yacht Basin on April 17, 1955. These leeches varied from 2.9 to 7.5 mm. in length, were dark brown in life, and easily detected on the host.

Six species of parasitic copepods have been taken from the body surface and pharyngeal cavity of the manini. *Lepeophtheirus dissimulatus* Wilson was the species most commonly encountered: 112 of 164 adult manini examined for parasites throughout the year were infested with from 1 to 20 of these copepods. The other parasitic copepods found were two species of *Caligus*, a *Dentigryps* sp., *Peniculus minuticaudae* Shiino, and *Nessipus costatus* Wilson, which encysts in the fins. A comprehensive report on these and other parasitic copepods from Hawaiian acanthurid fishes is being prepared by A. Lewis.

A mutualistic association was observed between the manini (and other reef fishes) and a small colorful wrasse, *Labroides phthirophagus* Randall. In the clear water off Manana Island two adult manini were seen being pecked over the head and body by this wrasse. The manini remained motionless in the water except for slight undulation of the fins. Since the stomach contents of several of the wrasses consisted primarily of calagoid copepods, it is believed that the fish were removing crustacean ectoparasites from the manini. On another occasion a manini was observed to swim directly to the "domain" of two of these labrids. As the manini was approached by one of them the surgeonfish was speared and brought ashore. Two adults of *Lepeophtheirus dissimulatus* were visible on its body.

DISEASES

The only data on disease were obtained from a series of unsuccessful attempts to maintain manini in an aquarium. Four adult fish were placed in a 23 gal. stainless steel aquarium which had previously been used to keep adult and juvenile manini for periods of several weeks. The water was aerated and filtered. Two days later two of the fish died, and on the following day the remaining fish were dead. Several hours before their death the manini swam in a disoriented manner. The fins were badly eroded. The head and body were excessively slimy, and large scattered sores were present. The fish were examined for parasites and found to have no more than the average complement.

The tank was cleaned (but not sterilized) and two more adult fish added. They died in a similar fashion in 48 hr. The tank was again cleaned and a 57 mm. juvenile manini placed in it. This fish died just 48 hr. later.

In spite of the filtration, the tank became cloudy on the second day after cleaning. A milliliter of the water was taken, successive dilutions made, and the higher dilutions cultured with a sea water and agar mixture (sterile aged sea water, agar, and a small amount of peptone and ferric phosphate). The number of resulting bacterial colonies were counted; the bacterial count of the original milliliter of aquarium water was computed at 212,000,000. Before the fish were placed in the aquarium the number of bacteria were probably less than 1,000,000 per ml.

Several smears were taken from eroded areas of dying manini. The dominant organism was a short, plump, gram-negative rod. It is not known whether this is the etiological agent of the disease or merely a secondary bacterium.

FOOD HABITS

Food of Larval Manini

Only three specimens of larval manini (6.6–7 mm. in total length) were available for an analysis of gut contents. Two of these fish were taken in a plankton net towed between 5:46 and 6:48 A.M. One was empty and the stomach of the other contained two appendicularian tunicates and a larval polychaete. The third fish was captured between 3:20 and 4:25 A.M. and was empty.

The digestive tracts of 57 manini in the acronurus stage (see section on transformation), which were obtained at night light stations in the Hawaiian Islands, Line Islands, and Phoenix Islands, were examined in the same way. Forty-five were completely empty. Four contained one to seven tiny fish scales; one of these also contained a shrimp chela. A few crustacean appendages (mostly from shrimp) were found in three other fish, one of which had also eaten a barnacle metanauplius. The intestines of two fish had a small amount of unidentified chitinous remains. The crustacean appendages, metanauplius and fish scales were not free in the gut lumen but were caught between longitudinal folds of the gut. It seems evident that the acronuri do not feed at night.

Four acronuri of *Acanthurus* were obtained from the stomachs of skipjack (*Katsuwonus pelamis*) caught during the day in Hawaiian waters. Because of their being partially digested, I am not able to identify any of these acronuri to species; two, however, are too large to be manini. The stomachs and intestines of all four of these fish were filled with zooplankton. Shrimps and shrimp larvae were the principal food items. Also found were copepods, polychaetes, and the remains of larval fish.

Food of Transforming Manini

In an aquarium, manini in their first day of transformation from the acronurus to the juvenile stage were not observed to feed. The digestive tracts of 30 specimens, collected in tide pools during the morning of their first day of transformation and preserved immediately, were devoid of food material. Of 24 similar specimens collected in the afternoon, 19 were empty, but 5 had eaten small amounts of fine filamentous algae and leptopel (for a discussion of leptopel see Fox, Isaacs, and Corcoran, 1951). Second-day transforming manini were seen to feed on algae in an aquarium, though not frequently, and preserved specimens of the same transformation age all contained small amounts of algae and leptopel. During the remaining 2 or 3 days of transformation, feeding is progressively heavier.

Food of Juvenile and Adult Manini

The gut contents of juvenile and adult manini consist almost entirely of relatively fine filamentous algae. The teeth of the manini are close-set and denticulate on the margins (Randall, 1956 *b*: fig. 2a) like other species of *Acanthurus*. They are therefore well adapted for feeding on filaments of algae. Experiments on feeding in aquaria showed that the absence of coarser algae in the gut contents is due to limitation in the size and strength of the jaws and teeth. Only the smaller branches of coarser algae, like species of *Hypnea*, were eaten. Small juvenile manini only ate the fine end branches whereas larger fish ate progressively larger branches.

Inorganic sediment was rarely found in the stomach or intestines of manini. When branches of a delicate species of the red alga *Polysiphonia* were mixed with fine sand and offered to aquarium manini, the fish were most adept at picking out the filaments which projected above the sand. The stomach of the manini is thin-walled, similar to that figured and described by Breder and Clark (1947: 295, fig. 1) for *Acanthurus coeruleus*. It contrasts sharply with the thick-walled, gizzard-like stomachs of some species of *Acanthurus*. Unlike the manini, the latter species normally ingest large amounts of inorganic sediment with the algae upon which they feed.

In addition to avoiding the ingestion of inorganic debris, juvenile and adult manini do not seem to feed on animal material (although some species of *Acanthurus*, such as *A. xanthopterus*, will accept animal food readily). Even when hungry, manini declined to eat any of several kinds of animal food which were offered. In an aquarium the fish were very skillful in avoiding the intake of small crustaceans and small masses of tunicates or sponges which were in close proximity to the algae on which they were feeding. Occasional small animals are found in the gut contents, however. These are probably taken in accidentally. In shallow water at Coconut Island, Oahu, an adult manini was observed feeding on algae close to an egg mass of the damselfish, *Abudefduf abdominalis* (the guarding fish had been frightened away). When the manini reached the edge of the egg mass, it ceased to feed, swam over the mass, and began feeding on algae on the other side. Other fishes, such as labrids and chaetodonts, feed greedily on the eggs when afforded the opportunity to do so by the absence of the guarding parent.

A study of the kinds of filamentous algae eaten by manini was undertaken. It was soon apparent that a great many different species of algae are eaten, and it is believed that at least a few filaments of virtually every filamentous alga in the Hawaiian area can ultimately be found in the gut of the manini if enough specimens are examined.

Dawson, Aleem, and Halstead (1955: 21), reporting on the gastrointestinal contents of 42 *Acanthurus triostegus triostegus* (size of specimens not given) from Palmyra, Line Islands, found 40 species of benthic algae and a number of species of diatoms of several genera. The number of algal species exceeded that previously known from Palmyra. Five species were most common in the stomachs: *Pterocladia* sp., *Sphacelaria furcigera*, *Lyngbya majuscula* (and/or *L. aestuarii*), *Bryopsis pennata*, and *Lophosiphonia* sp. The authors assumed that these were either dominant algae in the grazing grounds of the fish or were especially selected as food. It is the opinion of this author that these are the dominant algae, for (as is discussed below) the blue-green *Lyngbya majuscula* and another *Lyngbya* are not selected by this surgeonfish (at least not the Hawaiian subspecies).

A simple piece of apparatus was devised to test the preference by manini in Hawaii for various kinds of common filamentous algae. Ten tongue depressors were attached 2 cm. apart to a piece of wood. The free end of each depressor was notched and wrapped with a short piece of pliable galvanized steel wire. Different kinds of algae were fastened to the depressors by wrapping the wire ends around them. All 10 depressors with the assortment of algae attached were lowered simultaneously into the center of an aquarium in which juvenile manini, 26–30 mm. in standard length, were kept. When experiments were repeated, the position of the algae was always changed. If an alga was not eaten during the course of the experiment, it was left in the aquarium as long as it appeared edible to see if it would ultimately be devoured. The results are given in Table 3.

Many of the above algae were offered in a comparable manner to two adult manini, 123 and 128 mm. in standard length, with similar results.

Some species of algae not listed in the table were offered but not eaten; these, however, were probably too coarse for the juveniles. Included were two species of *Laurencia*, a species of *Gelidium*, a *Gracilaria*, and a species of *Dictyota*. A thallus of one of the species of *Laurencia* was placed in the aquarium with the adult manini. The small branches were eaten, leaving the major branches denuded.

Of the seven kinds of algae fine enough to be eaten but ignored in the preference experiments, one is a red (*Asparagopsis taxiformis*, well known for its high iodine content), one is brown (*Ectocarpus breviarticulatus*), and the rest are blue-greens. These were the only blue-greens tested.

Blue-green algae, some of which are the same species as those in the preference experiments, have been found in the stomachs and intestines of manini by the author (and, as noted, by Dawson, Aleem, and Halstead, 1955). This seems inconsistent with the results of the experiments. It was noted, however, that the blue-greens were never the exclusive food material, but were always mixed with large amounts of other algae, usually reds or greens.

In May, 1952, in water 10–20 ft. deep in Hanauma Bay, Oahu, the bottom was examined for the kinds of fine algae which reach a height of about 5 cm. or more. Three species this size were common: *Lyngbya majuscula*, *Asparagopsis taxiformis*, and *Plocamium sandvicense* (a red alga). Since surgeonfishes are abundant in the bay and at least two of the three algae are distasteful to one surgeonfish, the success of these algae might be associated with distasteful qualities.

Although there was little question from the observations that the manini requires no animal food, an experiment was designed to demonstrate that this species can subsist and grow on algae alone. A 23-gallon aquarium was divided into two compartments with a piece of plexiglass. Six manini, 26–31 mm. in standard length, were placed on each side and provided with cover in the form of several rocks grouped in the center of each compartment. The fish on one

TABLE 3

PREFERENCE FEEDING EXPERIMENTS ON JUVENILES OF *Acanthurus triostegus sandvicensis*

PREFERRED	COMPLETELY EATEN	SPARINGLY EATEN	NEVER EATEN
Polysiphonia sp.	*Hypnea* sp.	*Ectocarpus indicus*	*Lyngbya majuscula*
Enteromorpha sp.	*Hypnea* sp.	*Sphacelaria* sp.	*Lyngbya* sp.
	Lophosiphonia sp.	*Liagora* sp.	*Hormothamnion enteromorphoides*
	Ceramium sp.	*Jania* sp.	*Hydrocoleum cantharidosmum*
	Centroceras sp.	*Rosenvingia* sp.	*Calothrix confervicola*
	Gracilaria sp.	*Trichogloia* sp.	*Ectocarpus breviarticulatus*
	Rhizoclonium sp.	fixed diatoms (many species)	*Asparagopsis taxiformis*
	Dasya sp.		
	Enteromorpha sp.		
	Cladophora sp.		
	Grateloupia sp.		
	Herposiphonia sp.		
	Microdictyon setchellianum		

side were fed with a *Polysiphonia* and those on the other with an *Enteromorpha* (these were the algae upon which manini fed most vigorously in the preference experiments).

These algae are among the first macroscopic organisms to appear on the bottom of boats in harbor areas on Oahu. They are fast growing, especially the *Enteromorpha* which increased its length an average of 27 mm. per day on the eastern side of a boat during a period of 5 sunny days in April. If collected when the thalli first develop, they are almost devoid of animal life. A fresh mass of the *Enteromorpha* weighing 1.75 g. contained one ciliate, one nematode, one copepod, and a few epiphytic pennate diatoms and blue-green algal cells. Nevertheless the algae were thoroughly washed and picked over for animals before being fed to the fish. Fresh algae were added to the aquarium every day, and the previous day's algae removed. At the end of 2 weeks the fish were measured. Those fed on *Polysiphonia* grew an average of 2.9 mm.; those fed on *Enteromorpha* grew an average of 3.1 mm. During the 2-week interval the temperature in the aquarium was cool, varying from 23.0° to 23.8° C.

The preference experiments indicated that neither of these algae was eaten more readily than the other. Manini often alternated between feeding on the two. After 2 weeks of feeding on one of these, both kinds were added at the same time. It was immediately apparent that the fish had been conditioned to the alga on which they had been feeding. The "new" alga was untouched initially and only occasionally sampled an hour later. The preference was no longer obvious by the end of the day, however.

Manini feed almost constantly during the day, both in an aquarium and their natural habitat. They do not feed at night (see section on behavior).

The volume of algae consumed is large. Four juvenile manini, 28.5–45 mm. in standard length and weighing a total of 8.3 g., were fed a known mass of *Enteromorpha* in an aquarium early in the morning. The alga was weighed after firm squeezing followed by blotting on paper towels. At the end of the day the remaining fresh algal material was weighed in the same manner. Fresh *Enteromorpha* is grassy green and can easily be distinguished from fecal alga which is brownish or blackish green and tends to remain in pellets. The manini ate 10.8 g. of this alga one day and 8.8 g. the next. The same procedure was utilized for two adult fish, 123 and 128 mm. in standard length and 83.2 and 94.5 g. in weight, respectively. These two fish ate 27.4 g. of *Enteromorpha* in one day. The second day 16.3 g. of *Polysiphonia* was consumed. After being unfed during the morning of the third day, they ate 25.2 g. of *Enteromorpha* during the remaining 6 hr. of the day. Although these two adult manini in the above experiment were well adapted to aquarium life (they were reared to this size as captive fish in a pond of the Hawaii Marine Laboratory at Coconut Island and were maintained in the aquarium 12 days before the experiments), it was observed that they did not feed as frequently as adult manini in the natural environment (whereas the juveniles did). The feeding by the adults was readily interrupted by the approach of an observer. Usually only one fish fed at a time, and since the larger one dominated the smaller and held it in a corner of the aquarium for much of the day, the former consumed the major part of the algae. Yet both fish disdained to feed at all when placed in separate aquaria.

Stimulus to Feeding

The following simple experiments and observations were conducted in order to ascertain what sensory mechanism or mechanisms are utilized by the herbivorous manini in finding food.

The juice from several grams of *Enteromorpha* was squeezed into an aquarium in which two adult manini had been starved for a day. This was unfiltered and colored the water green when first dropped into the aquarium. No response was observed, even when some of the green color was seen to diffuse in the immediate vicinity of the nose and mouth of the fish. A similar experiment was performed on several juvenile manini with *Polysiphonia*, again with no visible response. By contrast, when an extract of *Polysiphonia* was dropped into an aquarium containing a half-grown *Abudefduf abdominalis* (omnivorous in food habits), this fish swam to the surface where the extract clouded the water red and snapped its jaws erratically in this region.

Some *Enteromorpha* and *Polysiphonia* was boiled to the extent that the algae began to disintegrate and lost most of their color. This was placed in the aquarium with fresh algae of the same kinds. Although juvenile manini fed initially on the fresh algae, the boiled algae was ultimately completely eaten.

Some maroon rayon fiber similar in texture and color to *Polysiphonia* was placed in an aquarium with juvenile manini. It was taken into the mouth temporarily by several of the fish. When the rayon was soaked in extract of the *Polysiphonia*, it was not taken in with greater frequency.

When recently voided fecal *Enteromorpha* was placed at the surface of the aquarium in the same manner that fresh algae were offered, most of the manini approached it, hesitated, and swam away. One juvenile drew a small amount into its mouth but hastily ejected it. When defecated filaments were added together with fresh filaments of *Enteromorpha*, only the fresh alga was eaten. In the absence of fresh algae, fecal algae which have remained in the aquarium for several hours may be ingested. The results of offering the blue-green algae listed in Table 3 were similar to that just described for recently voided fecal algae. The blue-greens were approached, but rarely taken into the mouth.

The nasal organs of a 26 mm. manini were cauterized with a hot wire. Five min. after this, the fish was offered some *Polysiphonia*. It fed on this with the same "enthusiasm" as previously.

Another juvenile fish was blinded by wiping a crystal of potassium hydroxide over the eye (other fish were blinded with silver nitrate crystals but these invariably died within 36 hr.). After contact with the potassium hydroxide, the surface of the eye became opaque white; this fish survived more than 3 days. It moved slowly about the bottom, occasionally swimming by chance into a mass of *Polysiphonia*. It never swam directly to the algae. When the algae touched the mouth it was often eaten. By the third day when the aimless movements carried the fish into a mass of algae, it fed voraciously.

It is concluded from the above that vision alone is needed to locate algal food, and the olfactory sense functions in feeding only to avoid unsavory material. Chemoreceptor organs in the mouth and possibly tactile organs as well also seem to be associated with the acceptance of algae and the rejection of material which is not utilized as food. The tendency to feed more on one alga than another develops after the algae have been sampled.

DIGESTION

In the work on nutrition of marine animals much effort has been expended on the analysis of mode of feeding and stomach contents, whereas little has been applied to the important aspect of the digestion of these animals. Yonge (1931) pointed out that information as to what an animal may collect and pass into its alimentary system may or may not indicate the true food of the animal. Thus, a study of digestion should logically accompany an investigation of food habits. The author is especially indebted to P. B. van Weel of the University of Hawaii for his counsel in the following research on digestion.

Morphology of the Digestive Tract

The similarity of the stomach of the manini to that of *Acanthurus coeruleus* as described by Breder and Clark (1947) has been mentioned. The manini stomach is elongate, and divisible into cardiac and pyloric portions. The cardiac part has prominent, longitudinal, irregularly scalloped folds on the inner surface; the pyloric part is smooth. A cross-section of the pyloric part showed the muscle tunic to be about the same width as the mucosa. There are few multicellular glands. The stomach wall is less than 0.1 mm. thick except posteriorly near the pylorus where it is slightly thicker than 1 mm.

Just posterior to the pylorus are five pyloric caeca. Several authors (including Yonge, 1931) have claimed that the pyloric caeca has taken over the role of the pancreas in certain teleosts, the latter organ supposedly being absent in these fishes. Dawes (1929) found that the pyloric caeca of the plaice (*Pleuronectes platessa*) had the same structure as the intestine with which it was in free communication, and Rahimullah (1945) came to the same conclusion after examination of 119 species in 50 different families of fishes. The structure of the pyloric caeca of the manini is consistent with the findings of Dawes and Rahimullah. The bile duct opens into the base of one of the pyloric caeca.

The pancreas of the manini was difficult to find. It was finally located in the form of two to four (usually three) small, round glands buff in color lying in the mesentery alongside the bile duct near its junction with the liver.

The intestine of the manini is long, in keeping with the well-founded biological principle that herbivorous animals have lengthy intestines. The length of the alimentary tract of large adult manini is nearly six times the standard length of the fish. Most of this length is attributable to the intestine which is complexly folded within the body cavity. The length of the alimentary tract of small juvenile manini is only slightly greater than three times the standard length of the fish. The increase of the alimentary tract relative to standard length is shown in the graph of Figure 3. With increasing size the volume of a body requiring nutriment increases faster than the intestinal surface if the rate of growth of the two is equal. A disproportionate elongation of the intestine is necessary to keep the area of absorptive surface adequate to the needs of the body. Hiatt (1947: 254, 257) noted a striking increase in the relative growth of the intestine of the herbivorous milkfish (*Chanos chanos*) between 90 and 115 mm. standard length. The ratio of intestinal length to standard

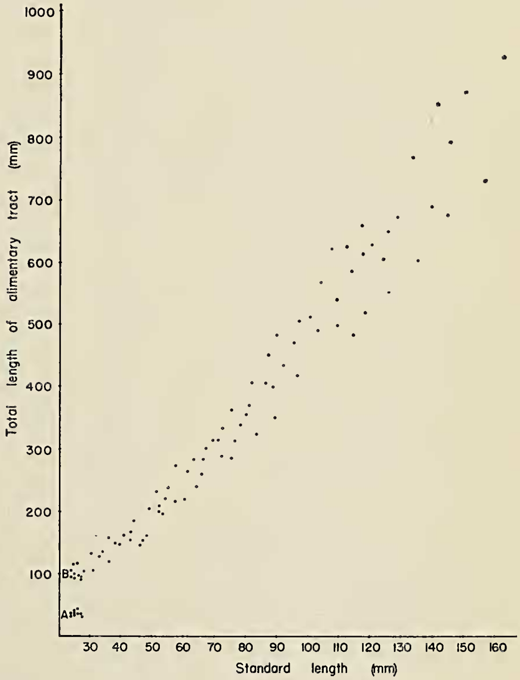


FIG. 3. Change in length of the alimentary tract of *Acanthurus triostegus sandvicensis* with increase in standard length. The group of points at *A* represents the length of the tract of 10 specimens (24–27.5 mm.) in the acronurus stage which were taken at a night light offshore. The points at *B* represent 10 tide-pool specimens (24–28 mm.) which have just completed transformation from the acronurus to the juvenile stage.

length increased from 3.5:1 to 7.2:1. He demonstrated a correlation between the increase in length of intestine and the substantial rise in the amount of larger algal types in the stomach contents and the reduced number of smaller food items like diatoms and blue-green algae. No sudden change-over in the size of algal food which is eaten by the manini occurs at any size range once transformation has taken place, and the curve of alimentary tract length plotted against standard length is without sharp inflection. The great increase of the gut length which occurs when manini transform from the acronurus to the juvenile state is discussed in the section on transformation.

The inner surface of the intestine is covered with small villi. The wall of the intestine is thin, its average thickness, not including any villi, is about 0.05 mm. The mucosa is about three to four times as broad as the muscle tunic.

Time for Algae to Pass through Gut

In order to find out the time which is required for algae to pass through the entire alimentary canal of the manini, two adults, 123 and 128 mm. in standard length, were fed only the red alga, *Polysiphonia*, for a period of 2 weeks. The tank was cleaned and the diet switched to the green alga, *Enteromorpha*. Two hr. and 25 min. later the fish were observed defecating the green alga. They had already deposited some on the bottom of the aquarium, so the following day the experiment was repeated by switching back to the red alga. In 2 hr. and 4 min. the first of the red alga was voided. In view of the great length of the digestive tract, this short interval of time seems extraordinary. However, when considered in the light of the nearly constant diurnal feeding and the volume of algae consumed, it becomes more understandable.

The same procedure was repeated for small juvenile manini, ranging from 26 to 30 mm. in standard length. The *Polysiphonia* passed through their alimentary tracts in 1 hr. and 45 min.

At night, when feeding ceases and the fish enter a state of torpor, the gut is not completely emptied in 2 hours or so. One 39 mm. manini, for example, which was caught at 1:15 A.M. still had a small amount of algae in the stomach and in the last 26 mm. of the intestine. The total length of the alimentary tract of this specimen was 177 mm. A 123 mm. manini was observed to defecate *Enteromorpha* 14 hours after it last fed on this alga.

Digestion of Algae

Lefèvre (1940) has shown that different kinds of algae resist digestion by gastrointestinal juices of fishes in various degrees. Although supporting growth of manini as well or better than the *Polysiphonia*, the *Enteromorpha* appeared less digested. Filaments of this alga were found to be only slightly altered after their rapid passage through the gut. The cellulose cell walls seemed unaffected, and the cell contents still in place. The only discernible change in most cells was the breaking up of the parietal grassy green chloroplast to brownish-green granular clumps. A visual comparison was made of the quantity of starch granules in the *Enteromorpha* cells following staining of fresh and fecal algae, and no obvious differences were apparent. Clearly, more work is needed to elucidate the problem of algal nutrition of the manini. The possibility that the pectic sheath material of algae is digested should be investigated.

Digestive Enzymes

No reference was found in the literature to any assay of the digestive enzymes of a strictly herbivorous fish. From work on herbivorous animals other than fishes the generalization can be made that proteinase is less active in herbivorous forms than in carnivores and amylase more active. There are indications that this is true for fishes, at least for amylase. Kenyon (1925) compared starch digestion in the carp (*Cyprinus carpio*) which, though omnivorous, eats large amounts of algae, and the carnivorous pike (*Esox lucius*). He wrote, "... the carp, which is largely a vegetarian, possesses amylase in tremendous amounts in the hepatopancreas and to a less extent throughout the intestinal mucosa. The pickerel, on the contrary, ... possesses only a negligible quantity of amylase, having little in the pancreas, esophagus, intestine, and practically none in the stomach." Vonk (1927) wrote that the carp has more than 1,000 times the amount of amylase in the pancreas than that of the carnivorous pike or shark. Schlottke (1939) found amylase in large quantities in the carp, whereas the predaceous rainbow trout (*Trutta iridea*) and perch (*Perca fluviatilis*) evidently produced almost no amylase. Data comparing the activity of proteinase and lipase of omnivorous and carnivorous fishes are meager and conflicting.

In view of the importance of the hydrogen ion concentration to enzyme activity, the pH of the contents of various parts of the digestive system of the manini was determined. The measurements of pH were made with a Beckman pH meter on six adult fish which averaged 120 mm. in standard length. The results, expressed in the ranges of pH found, are given in Table 4.

TABLE 4

pH OF ORGANS OF THE DIGESTIVE SYSTEM OF *Acanthurus triostegus sandvicensis*

ORGAN	RANGE OF pH
Stomach	6.3–7.7
Duodenum	7.7–9.1
Intestine	8.0–9.1
Gall bladder	6.2–6.4

The variation of pH within any one organ appears to be correlated with the degree of fullness of the organ. The low pH values were found in the organs when they were filled with algae. Hydrochloric acid secretion in a stomach in which food is present is a probable explanation for the greater acidity at this time. Babkin and Bowie (1928) found a variation in pH of the duodenum of the killifish (*Fundulus heteroclitus*) similar to that shown above for the manini. These authors also noted that low values of pH were obtained when the duodenum contained food. They attributed this to the discharge of bile to the organ when filled with food.

Extracts for the enzyme study were consistently prepared from the stomach (both cardiac and pyloric portions combined), pancreas, pyloric caeca, duodenum, and intestine of adult manini which were killed immediately before the removal of these organs. Because of the excessive thinness of the gut wall, it was very difficult to separate the mucosa from the muscle layers; therefore extracts were made of entire organs or linear parts of organs. All portions of the digestive tube to be extracted were first washed with sea water to remove food material. Tissues were ground in mortar and pestle with calcareous sand. This sand had previously been cleaned by repeated washings with water, boiling with 3 per cent potassium hydroxide and then for a short while with 2 per cent hydrochloric acid. In view of MacKay's (1929) report that 30 per cent alcohol yielded the most active amylase from the eel pout (*Zoarces anguillaris*), this agent was also used to extract amylase in the present study. Lipase extracts were made in 40 per cent glycerol and protease extracts in 50 per cent glycerol. Extraction was carried out in a refrigerator for a period of 24 hr.

Digestion by amylase and lipase proved to be rapid at room temperature (26°–27° C.); thus no incubation was necessary in experiments with these enzymes. Digest tubes with protease were incubated at 36° C.

Buffer solutions used in the digestion experiments were based on the mixtures of Clark and Lubs (Hawk and Bergeim, 1942: 24). Bacterial action was prevented by the addition of several drops of toluol to the extract and digest test tubes.

The substrate for amylase experiments was 1 per cent starch solution. To each test tube containing 1 ml. of extract of the digestive organs 5 ml. of starch solution and 1 ml. of buffer of pH 6.8 were added. For each tissue there was a control tube identical with the experimental digest tube except for the previous boiling of the extract to inactivate all enzymes.

The progress of digestion was followed by removing small amounts of fluid from the digest tubes and testing with Lugol's solution. The changes in the solution from deep blue-black through purple, red, yellow, and finally colorless indicated a breakdown of the starch at least to achroodextrine. Ultimately all of the tubes were colorless, thus disclosing starch digestion by the pancreas, pyloric caeca, duodenum, intestine, and stomach. The experiment was repeated three times with sections of the digestive tract vigorously washed to minimize the possibility of enzyme from another source being adsorbed on the epithelial surface of the organ being tested.

Again, there was a definite amylase reaction from each organ.

The positive results seem unusual in view of the fact that most vertebrates (except for mammals which secrete ptyalin in their saliva) break down starch initially with pancreatic amylase and complete the process with intestinal maltase. These results on the manini seem less dubious, however, in the light of the finding by Kenyon of amylase throughout the whole gut of the carp (although it was considered to lack a true stomach) and by the detection of stomach and duodenal amylase in *Zoarces* by MacKay. Also Babkin and Bowie found amylase in the intestine of the killifish. They were certain it was not adsorbed pancreatic amylase, for they were unable to observe any proteolytic action in the same extract.

Pancreatic amylase of the manini is nearly 20 times more powerful per unit of tissue than the amylase from other organs, while that from the stomach was weakest (attempts were made to obtain extracts from equal amounts of glandular tissue of the organs under comparison).

The pH optimum of the amylase, as determined by color change with Lugol's solution and the micro method of Linderstrøm-Lang (Linderstrøm-Lang and Holter, 1933), is 6.7.

The Schoorl method was utilized to test for the presence of maltase in the stomach, pyloric caeca, pancreas, duodenum, and intestine of the manini. One per cent maltose solution served as the substrate. Trials for all organs were run at pH 7.0 and 7.2 and incubated at 30° and 35° C. for periods up to 12 hr., but results were consistently negative.

The method of Michaelis and Rona (see van Weel, 1937: 245) was used in lipase experiments. Tri-n-butyrin solution was used for the substrate. Digestion occurred rapidly in all the organs tested. It was evident that the pancreas produced the most lipase and the stomach the least, although the difference was not as marked as with amylase. The pyloric caeca showed the greatest lipase activity of the remaining organs. Difference between the duodenum and the rest of the intestine was not discernible. The pH optimum determined for pyloric caeca lipase of the manini is 7.2.

Detection of protein digestion was based on the formaldehyde titration of Sörensen (Jordan, 1927). The substrate was a 3 per cent colloidal solution of gelatin.

In initial experiments protease was found in the pancreas, pyloric caeca, duodenum, and intestine, but not in the stomach. In none of the organs was the proteolytic activity strong. The pH optimum of pancreatic protease is 8.4.

Because of the acidic reaction in the stomach of the manini and the knowledge that protease in this organ can vary widely from individual to individual depending on the state of hunger of the animal (Schlottke, 1939), further effort was expended to localize this enzyme in the stomach. Extract of high concentration (prepared from trituration in 5 ml. of 50 per cent glycerol of three adult manini stomachs, two of which contained considerable algae) finally gave positive results. One ml. of this concentrated extract (thus containing the extractable enzyme from three-fifths of a stomach) at pH 6.0 yielded acid equivalent to 0.2 ml. of 0.015 normal sodium hydroxide after 4 hr. of incubation.

A piece of the very thin covering (one cell layer thick) from one of the internal rings of an onion was peeled off and placed in a glass stender and covered with the fluid from the intestine of an adult manini. The onion skin was examined after 24 and 48 hr. periods, but no digestion of the cellulose cell walls occurred. The experiment was repeated with fluid from the intestine of another adult specimen, again with negative results. Thus there appears to be no cellulase-secreting micro-organisms in the intestine of the manini.

It is concluded that the results of the enzyme study of the manini are consistent with the generalization previously made concerning the digestive enzymes of herbivorous animals except for the absence of cellulase.

REPRODUCTION

Sex Ratio

No sexual dimorphism in external morphology was noted; therefore gonad examination was necessary for sex determination. The gonads lie in the ventroposterior part of the body cavity. No difficulty was experienced in distinguishing an ovary from a testis macroscopically except with immature fish. The ovaries are pinkish cream in color, smooth, slightly compressed laterally, and closely applied to one another in the mid-line. The testes are white, strongly compressed, irregularly lobular, and in contact with each other only ventrally.

It was apparent from sampling the catch of trap fishermen throughout the year that approximately twice as many male manini as females were taken. In the month of May, 1953, 291 trap-caught adult fish were sexed; 68 per cent of these were males. The traps in which the fish are caught are unbaited. A typical trap consists of a rectangular framework (about 2 × 5 × 6 ft.) of steel rod covered with chicken wire. A cone of chicken wire with a narrow slitlike opening extends inward from one end to about the center. Some trap fishermen prefer to leave one or two butterfly fish or other fishes of little economic value in the trap in the belief that other fishes will be more prone to enter. If male manini are more gregarious or less cautious or more migratory than females, they would be caught in traps with greater frequency than females; therefore sex ratios ascertained from trapped fish should be viewed with caution.

The sex was determined for 221 adult manini from islands in the tropical Pacific in the collections of the U. S. National Museum, the Bernice P. Bishop Museum, and the University of Hawaii. Most of these specimens were taken with rotenone, seine, and throw net. These collective techniques are less selective than traps and the sample would seem to be a better indication of true sex ratio. Of the 221 fish, 134 (60.7 per cent) are females. A chi-square value of 10 results from testing whether 134 females could be obtained from 221 fish randomly sampled from a population in which the true sex ratio is 50-50. This high chi-square has a probability greater than 0.01 that a sample more extreme than the above could be drawn by chance from a half male, half female population; thus the hypothesis of a 50-50 sex ratio is rejected.

It is nevertheless possible that the apparent predominance of female manini is spurious. Most of the 221 specimens were taken in inshore areas. The traps from which 198 males of 291 manini were caught were set in from 30 to 90 ft. of water. Perhaps females are more abundant in shallower water and the males predominate over deeper parts of the reef. More collections are needed to clarify this problem.

The museum collections of manini offer some slight evidence for differential schooling by sexes. One sample of 7 manini from the outer reef at Eniwetok Atoll, Marshall Islands, is entirely male; another of 12 fish from the lagoon of Kwajalein Atoll in the Marshalls is wholly female.

Spawning Cycle

The manini in the Hawaiian Islands has a distinct spawning season. This has been ascertained by the examination of the gonads of adult fish and collections of young throughout the year. In more equatorial areas, on the contrary, the spawning of this surgeonfish appears to be year-round. There is also evidence both in Hawaii and the Gilbert Islands that the pattern of the incoming young correlates with the lunar cycle. This is attributed to a lunar effect on spawning by adults.

From October 31, 1952, to October 27, 1953, a total of 137 female and 156 male manini 100 mm. or more in standard length were purchased in 41 samples from a fisherman for the purpose of examination of the gonads. The fish were caught in traps set in depths of 30–90 ft. from Kewalo Basin to Koko Head, Oahu. The length of the gonad on each side of the body cavity of each specimen was measured and the average length recorded. This average measurement was divided by the standard length and the quotient multiplied by 100. The range and mean of the resulting percentages are presented in Table 5.

Although the monthly samples are small, it is nevertheless apparent that the gonads of both sexes undergo a significant change in relative length during the year. They are largest in late winter and spring and smallest in late summer and early fall. The change which takes place in the ovary in late July and August is more complex than would be indicated from a mere shortening. The ovary (presumably following the last spawning) is red, flattened, and has a large lumen. Residual eggs are gradually absorbed (eggs being absorbed appear as amorphous masses of variable size), and the entire organ regresses to small size and a translucent gray color. There is

TABLE 5

GONAD LENGTH AS A PERCENTAGE OF STANDARD LENGTH BY MONTH, 1952–53

MONTH	NO. OF FEMALES	$\frac{\text{GONAD LENGTH}}{\text{STANDARD LENGTH}} \times 100$		NO. OF MALES	$\frac{\text{GONAD LENGTH}}{\text{STANDARD LENGTH}} \times 100$	
		Range	Mean		Range	Mean
Oct.	15	7.1–18.2	9.4	14	5.6–22.8	9.4
Nov.	2	7.7–14.4	11.1	12	8.3–22.8	15.5
Dec.	4	12.3–25.0	14.3	11	10.0–22.1	15.9
Jan.	9	8.6–25.6	13.5	10	8.4–25.0	17.9
Feb.	15	14.1–25.6	18.2	31	20.4–34.5	28.6
Mar.	19	13.5–32.2	19.3	25	12.8–35.7	28.6
Apr.	17	10.4–26.4	17.3	7	22.8–38.5	29.4
May	6	9.8–23.3	16.2	5	18.2–31.2	25.6
Jun.	9	7.0–34.5	13.5	5	15.0–25.1	20.0
Jul.	10	7.5–17.6	9.6	9	8.1–26.3	14.9
Aug.	9	5.5–11.9	7.2	8	6.5–23.8	13.2
Sept.	22	5.0–14.5	8.4	19	7.6–17.3	9.0

variation in the time when this occurs in individual fish, hence the ultimate small size is not apparent when the values of a number of fish are averaged by month. The ovary of a 145 mm. female taken on August 7, for example, was only 8 mm. in length.

The gonad measurement data are more significant in indicating a definite spawning season of the manini when coupled with the results of sampling the young throughout the year. Transforming and small juvenile specimens were absent from inshore areas during the fall and early winter months of 1952–53. Extensive observation and collecting were undertaken during the winter and early fall to ascertain the time of the first and last arrivals of acronuri from the pelagic realm. The first transforming young were sighted on February 14; the last of the season straggled in on October 6. In 1954 the first young were discovered on February 9. During my absence from the state, my wife and Philip Helfrich made an effort to determine the date of the last influx of young in 1954. In October only a single small juvenile was collected; it was taken on the 9th of the month and measures 27.5 mm. in standard length. It is completely transformed; therefore it had been in the tide-pool zone for about 5–8 days (see sections on transformation and growth). The first transforming young of the 1955 season were observed on January 27.

The time between the finding of the first ripe female of the season and the first incoming young and the time between the last ripe female and the last incoming young constitute estimates of the duration of larval life. The last ripe female of the 1952–53 season detected in the sampling program (see Table 6) was found on July 21. The first ripe female of the 1953–54 season was found on December 1. The last ripe females of this season were observed in the July 16 sample. The three estimates of the duration of larval life from the above data are 71, 78, and 83 days. Admittedly such estimates are subject to considerable error. Their average, 77 days, approximates 2½ months.

In order to obtain quantitative data on the recruitment of young to inshore areas of Oahu, a single large tide pool at Diamond Head (Fig. 4) was chosen for repeated collections of manini. This pool is nearly isolated at low tide. An overhanging ledge on the left (east) side of the pool provides excellent cover for the small fish. Pools as large as this but lacking such cover contain fewer manini. Each week at low tide the narrow outlet to the sea was occluded with a net, and all the manini in the pool were poisoned with rotenone. A total of 157 manini less than 30 mm. in standard length were taken from the pool during the season (Fig. 5). Nineteen specimens 30 mm. or longer were collected; these are presumed to have been in the tide-pool zone for more than one week (see section on growth) and hence are probably migrants from adjacent pools. They are not included in

FIG. 4. Tide pool at low tide at Diamond Head, Oahu, from which the collections of *Acanthurus triostegus sandvicensis* of Figure 5 were made.

the graph of Figure 5. The poison stations on August 13 and August 21 were interrupted by unexpected large waves, and no fish were collected. However, on these two dates manini were counted in the pool before rotenone was added and these numbers are indicated by the dotted line on the graph. Probably there were at least twice as many small manini in the pool as are recorded, for most of the fish take cover rapidly when an observer approaches and are hidden before they can be counted. The sample of 36 fish taken on September 12, on the other hand, may be higher relative to the overall number of tide-pool young at this time than it should be. Observation of other pools at Diamond Head and along the shore of the Ala Wai Yacht Basin prior to, during, and after September 12 failed to disclose any striking influx of young. Nevertheless, the number of incoming young in September is high and this month should be included with the period May to August as indicating large tide-pool recruitment on Oahu.

Although this sampling from a single pool is not sufficiently great to be correlated closely with the similarly inadequate samples of adult gonads, the May to September recruitment seems to correspond roughly to the greater degree of gonad development from February to June.

In more equatorial waters the *A. triostegus triostegus* appears to spawn throughout the year. The 221 adult fish used for the sex ratio determination were collected mostly from the Mari-

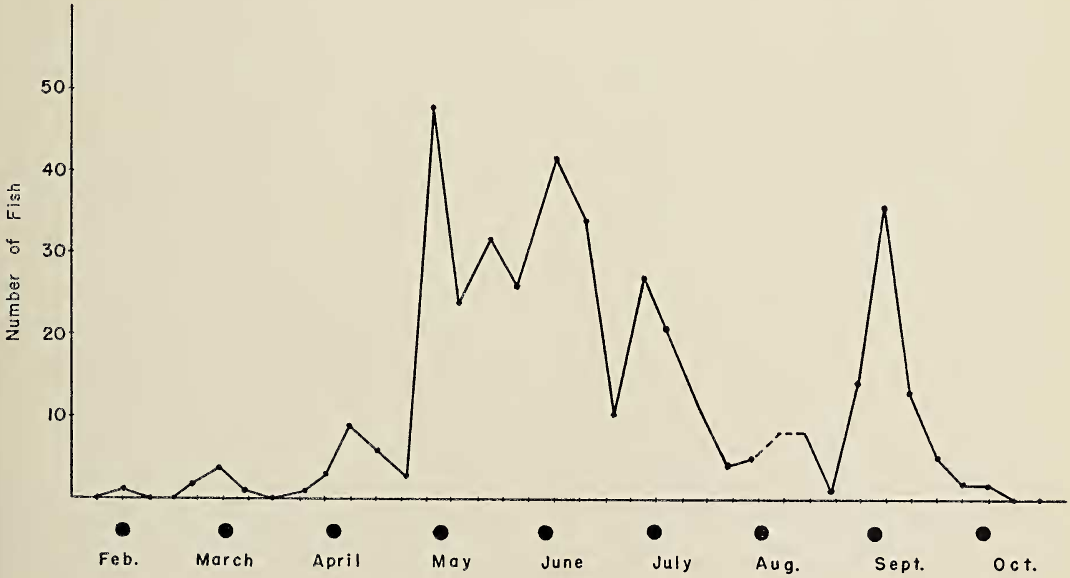


FIG. 5. Weekly collections of *Acanthurus triostegus sandvicensis* made in 1953 from a single tide pool at Diamond Head, Oahu. Only specimens 30 mm. or less are recorded. Times of new moon are indicated by black circles.

ana, Marshall, Gilbert, Line, and Phoenix islands—groups in which the sea surface temperature exceeds 80° F. (26.7° C.) the year-round and where the annual variation in sea temperature is slight (based on Hydrographic Office, 225). Examination of these fish revealed ripe gonads in every month of the year. Specimens of transforming or small juvenile manini collected every month of the year from these areas were found in museums.

It is, therefore, puzzling that the seasonal spawning in the Hawaiian Islands seems to be associated with the colder part of the year. The mean monthly sea surface temperatures around Oahu (1945–55) vary from about 75° to 81° F. in an average year (Leipper and Anderson, 1950; Hydrographic Office, 280.) The temperature of the warm part of the year is essentially the same as that of the lower latitudes where spawning is year-round. The initial enlargement of the gonads in Hawaii coincides with the time of decreasing sea surface temperature in the fall. The marked increase in tide pool recruitment in May appears to correspond to increased spawning in February–March, the time of coldest water temperature.

If temperature or some other factor such as change in length of day is the cause of interrupted spawning in Hawaii, then manini in a region of the South Pacific Ocean with comparable latitude should spawn seasonally and 6 months out of phase from Hawaiian manini. Unfortunately no data are available from southerly island groups such as the Australs or southernmost Tuamotus where sea temperatures closely approximate those in Hawaii.

Small juvenile and transforming *A. triostegus triostegus* were taken or observed by the author in every month of the year (1956–57) in the Society Islands (where temperatures range from about 77.5° to 81° F., or 25.2°–27.2° C.). The manini is not as abundant in the Society Islands as in Hawaii, and the insignificant tide in the former island group made it difficult to find numerous individuals isolated in tide pools. Collections were insufficient to demonstrate any possible variation in reproductive activity during the year.

A cyclic fluctuation in the abundance of incoming young within the spawning season in the Hawaiian Islands is apparent from Figure 5. The peaks of these fluctuations line up roughly with the time of new moon. This correlation is more evident from the extensive collections made from various tide pools plotted in Figure 6. The large mode of May 10 centered on a standard length of 26 mm. contains 54 transforming fish. The time of new moon was May 13. The large mode of April 17 is centered on a standard length of 27 mm. and contains 10 transforming manini. New moon in April occurred on the 13th day.

Tester and Takata (1953: 36, fig. 14) have demonstrated a similar lunar periodicity in the appearance of young aholehole (*Kuhlia sandvicensis*) in tide pools on Oahu.

If the periodicity in the influx of manini acronuri is a function of some lunar effect on the young and not on the spawning adults, then the peak fluctuations of incoming acronuri in areas of different temperature, and hence different rates of development (see development section), should still correlate with the time of new moon. A sample of 108 small manini collected with rotenone by the author from tide pools at Onotoa Atoll, Gilbert Islands, on August 21, 1951 (Fig. 7), demonstrates that this is not the case. Onotoa is located in the central Pacific (1° 47′ S., 175° 32′ E.); the monthly mean sea surface temperatures vary only slightly from 82.5° F. (28.6° C.) throughout the year. Full moon occurred on August 16 (new moon on August 2). The large mode of Figure 7 centered on about 23 mm. standard length includes only 9 transforming specimens which average 23.5 mm. in standard length. Thus the peak influx of the fish comprising this mode is estimated at 4 or 5 days prior to August 21. This large Onotoa sample, therefore, is about 11 days out of phase with the lunar cycle of incoming young on Oahu (where the mean monthly sea surface temperatures vary from 75° to 76.5° F., or 23.9°–24.5° C., from January to April).

In order to obtain direct evidence of lunar spawning by adult manini and to more sharply delimit the spawning season, the entire catch of two trap fishermen was examined for ripe fish on 62 days from June 19, 1953, to September 3, 1954. The catch was usually brought to port alive. The fishermen would not permit the opening of the body cavity without purchasing the fish, but they allowed pressure to be applied to the abdomen of each manini.

When running ripe males (the sperm of which were motile) were discovered in samples taken throughout the year, it was realized that the limits of the spawning season could not be defined by the development of the male gonad. As would be expected from Table 5, however, there were more ripe males during the spawning season than outside of it. Of 745 adult manini (since trap caught, an estimated two-thirds were

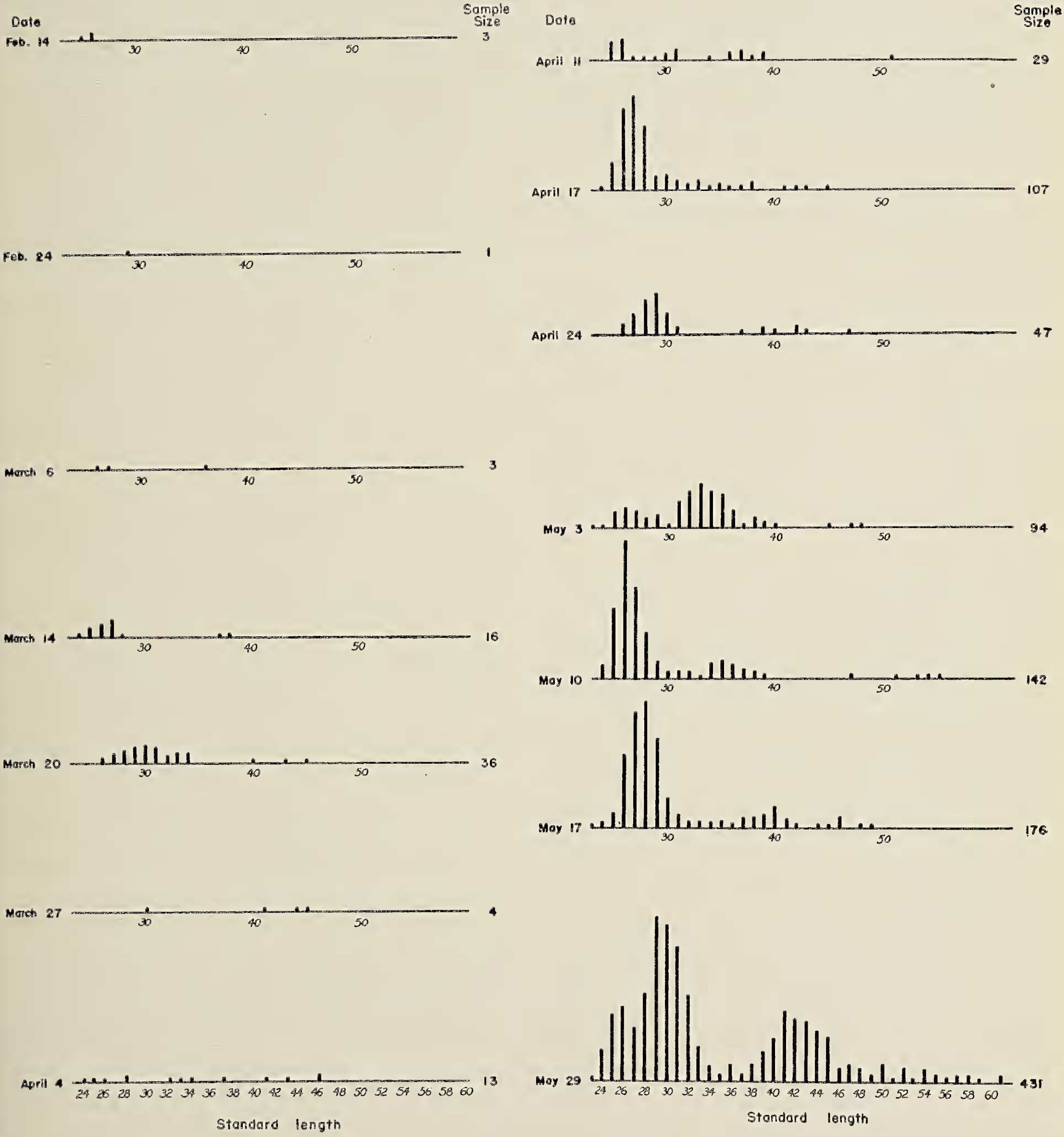


FIG. 6. Tide-pool collections of *Acanthurus triostegus sandvicensis* from Ala Wai Yacht Basin to Makapuu Point, Oahu, 1953. Vertical distance between horizontal lines is proportional to number of days between samples.

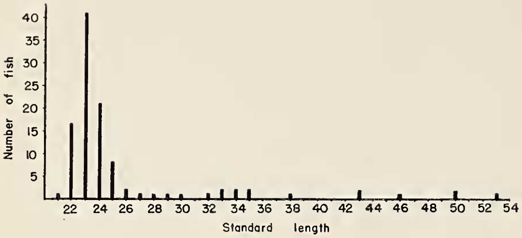


FIG. 7. Collection of *Acanthurus triostegus triostegus* from tide pools of the outer reef flat, Onotoa Atoll, Gilbert Islands, August 21, 1951. Sample size, 108. Nine specimens 21–25 mm. in standard length are transforming from the acronurus to the juvenile stage; the rest are juveniles. Time of full moon, Aug. 16.

males) examined from September to November, 11.8 per cent were running ripe males; 23 per cent of 2,419 adult manini (an estimated two-thirds of which were males) examined from February to June were running ripe males. No variation in degree of ripeness was apparent within the period of a single month. It should be emphasized, however, that no sharp dividing line exists between the condition of a running ripe male and one that is not quite running ripe, and these data tend to be subjective in this regard.

Ripe females are more easily distinguished. Fertilizable eggs of female manini are about 0.7 mm. in diameter, prefectly transparent, and are released when the abdomen is only slightly squeezed. The data on ripe females in terms of the lunar month are summarized in Table 6. As may be seen in this table, the number of fish examined on the different days ranged from 9 to 252. This variability is entirely due to variation in the catches. Also there is no regular sequence in time when the catches were examined. Scheduled sampling was not possible largely because of the great dependence of trap fishing on hydrographic conditions. In addition to being impeded by rough seas, trap fishermen are restricted by turbid water (traps are not found by surface markers but by observing through a glass-bottom box). Although the fishermen ordinarily tend their traps twice a week, they may be held in port several weeks by dirty water. A successful sampling day was also contingent on being at Kewalo Basin when the catches were unloaded. Frequently the fishermen came in unexpectedly early and their fish were promptly taken to market. Market fish were not sampled because catches of previous days may accumulate and the date when fish are caught is usually not available.

A total of 43 running ripe females were found. Thirty-nine of these were taken from 12 days before to 2 days after the full moon and only 4 from the remaining half of the lunar month. A total of 2,552 adult manini were examined in the former period, however, and only 1,311 in the latter; therefore a correction is necessary for this discrepancy in sample size. A corrected figure of 7.8 ripe females instead of 4 is the proper number to compare with 39. Nevertheless, it still remains obvious that a significantly greater number of ripe females, and hence probably greater spawning, occurs before and shortly after full moon than before and shortly after new moon. Since at least a few acronuri of all sizes (see section on transformation) enter tide pools at all times during the month and not totally in one portion thereof, some spawning might be expected throughout the month.

One sample of adult manini was examined on July 29, 1955. There were 7 running ripe female fish among the 57 manini comprising the sample. Full moon occurred on August 3.

It is not known whether spawning by the same fish takes place every month. There is evidence, however, that individual fish spawn more than once a season. The long season in itself suggests repeated spawning. If large ripe females were found at the start and progressively smaller ones throughout the rest of the season, a long spawning season might be indicated with each individual spawning only once, but no obvious trend in size of the 43 ripe females was apparent. The first ripe female of the season, which was found December 1, measured 138 mm. in standard length. The last (July 21) was also large, 140 mm. The shortest found were 106 mm. (March 13) and 101 mm. (July 14). More convincing is the failure to see any completely spent ovaries in fish during the spawning season and the observation of spent and regressing ovaries in all of the females at the end of the season. The strongest evidence concerns the finding in ripe females of a second mode of egg size

TABLE 6

RESULTS OF SAMPLING FOR RIPE FEMALE *Acanthurus triostegus sandvicensis* DURING THE SPAWNING SEASON

DATE	DAYS TO NEAREST FULL MOON		NO. OF FISH EXAMINED	NO. OF RIPE FEMALES
	Before	After		
Jun. 19, 1953	8		40	1
21	6		9	1
Jul. 14	12		114	1
17	9		45	0
21	5		14	1
Dec. 1		11	141	1
8	12		126	1
22		2	139	0
29		9	96	0
Jan. 8, 1954	11		149	1
12	7		21	1
24		5	26	0
Feb. 5	12		30	0
9	8		30	0
12	5		41	1
Mar. 2		13	31	0
12	7		144	6
30		11	44	0
Apr. 2		13	87	0
6	12		198	0
9	9		121	0
13	5		111	0
16	2		193	7
20		2	132	6
23		5	76	0
27		9	151	0
May 1		13	88	0
6	11		83	1
11	6		226	3
14	3		149	2
18		1	18	0
21		4	204	1
25		8	159	0
28		11	103	2
Jun. 11	5		42	2
18		2	97	0
22		6	29	0
25		9	49	0
Jul. 2		14	27	0
9	7		28	0
16	0	0	252	4

about half the size of the ripe egg mode, coupled with the knowledge that this mode is not retained in the ovary through the summer months. This mode of intermediate-size eggs appears to be a persistent unit within the ovary of all mature female manini during and 1–2 months before the spawning season, suggesting that it constitutes a static mass of eggs from which modes of ripe eggs may develop periodically. It is not known whether this mass is built up constantly or at short intervals from the huge reserve of minute primordial eggs which is present in the ovary of every adult female regardless of the time of year (and is here not considered as a mode of egg size).

The procedure for the determination of egg diameters was as follows: Tiny sections were snipped from various parts of an ovary (which was previously preserved in 8 per cent formaldehyde solution) and placed in water in a Syracuse watch glass; the eggs were teased from the ovarian tissue with dissecting needles; the egg diameters were then measured with an ocular micrometer at × 24. Many of the eggs were oblong, probably because of unequal pressure of adjacent eggs at the time of preservation. Instead of measuring the greatest or least diameter, the eggs were moved into position by moving, but not turning, the watch glass on the micrometer image which remained fixed in a horizontal position. This method reduces the possibility of bias but has the disadvantage of increasing the spread of modal groups on graphs of egg diameter measurements.

Graphs of the egg diameters of ovaries from 9 adult female manini are shown in Figure 8. These graphs do not show any definite sequence.

Graph *C*, of a 15 mm. ovary from a female taken on January 2, for example, portrays the egg diameter pattern of an immature but maturing ovary. No graphs were made of egg diameters of ovaries from adult fish taken in August because the fish have only primordial eggs about 1 to 3 micrometer units (.035 to .105 mm.) in diameter except for those in which larger eggs are being resorbed. The relative size of the group of primordial eggs was estimated only for the ovary graphically illustrated in *A*.

Except for the immature gonad of *C*, all of the ovaries display a mode of egg size centered on about 10 to 12 micrometer units in diameter. This prompted the examination of samples of eggs from 54 ovaries taken from female fish throughout the year (more, however, from mature females during the spawning season). Sufficient eggs from each ovary were measured to determine the presence of obvious modal groups. A definite mode at from 9 to 12 micrometer units in egg diameter occurred in 46 of the ovaries, 15 to 35 mm. in length, from fish caught from September 15 to July 21. The median of this mode of 38 of these fish appears to lie between 10 and 12 micrometer units. In the ovaries of 8 fish, the median lies between about 9 and 10 units. One of these fish is the only running ripe female of the 54 examined. The remaining eight fish lack an intermediate-size mode; all of these have small gonads. No specimens were found among the 54 females with a group of eggs which have an average diameter greater than 12 units but less than the 20 to 21 unit average size of ripe eggs. Also, when checking for ripe females among the 3,863 adult manini of Table 6, the eggs pressed from the body cavity of few, if any, of these were of a size between that of the usual mode and the ripe egg mode. It is expected that such a size would be extruded with moderate pressure on the abdomen of the fish, since eggs of about 10 micrometer units (0.35 mm.) are frequently forced out. Eggs as large or nearly as large as completely ripe eggs, but in which small opaque white regions were visible, were seen almost as often as the ripe, perfectly transparent eggs. These can not be fertilized, and females containing them were not considered among the ripe fish previously discussed. The failure to find a mode of eggs intermediate in size between about 10 and 20 micrometer units suggests that eggs maturing from the former modal group (the eggs of which are opaque) do so rapidly. Perhaps the enlargement is essentially a process of hydration.

In view of the finding of so few female manini with fertilizable eggs during the season, it is further believed that the ripe eggs are not retained very long in the ovary. Admittedly a change in behavior of ripe females might influence the frequency with which they enter traps (a possible cessation of feeding, however, would not seem to affect the rate of entry, for the traps, as mentioned, are unbaited). Also, confinement in the traps might affect the maturation of the eggs.

If, however, it is assumed that ripe eggs are held within a female no longer than 1 day on the average, and 43 ripe female fish is the number that would be present in truly random samples of the population equal in size to the ones taken, then the small number of ripe females actually constitutes an indication that every adult female spawns once each lunar month. Since the lunar month is 29.53 days, only about one-thirtieth of the females sampled from the population during the spawning season would be ripe. As mentioned, 3,863 adult manini were examined during the 1953–54 season, an estimated one-third of which, or 1,288, were females. One-thirtieth of 1,288 is 43, precisely the number of ripe females which were found.

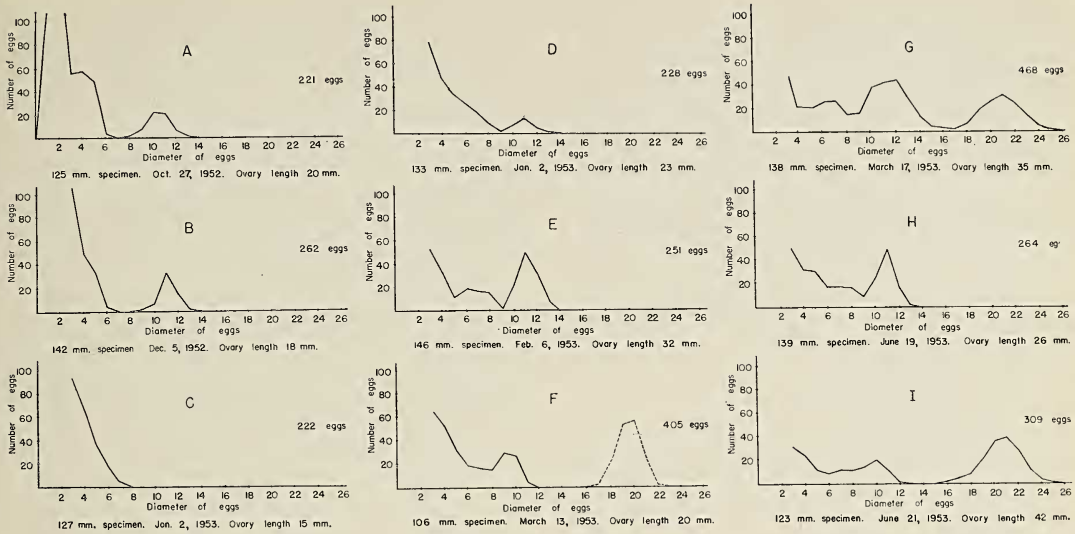


FIG. 8. Egg diameters of *Acanthurus triostegus sandvicensis* plotted as units of an ocular micrometer. Scale: 1 unit = .035 mm. Except for *A,* where the number of eggs of 1 and 2 micrometer units were estimated at 1,575 and 627, respectively, no eggs less than 3 micrometer units were measured.

Spawning

The spawning of *A. triostegus sandvicensis* was never witnessed, in spite of considerable observation both at night and during the day and at various times of the month. On June 12, 1957 (full moon) *A. triostegus triostegus* was observed to spawn at the atoll of Tikahau in the Tuamotu Archipelago at dusk (5:30 P.M.). It is believed that the failure to see the Hawaiian manini spawn was due to the lack of effort at dusk. The following account of the reproduction of the Tuamotu manini is probably similar to that for the Hawaiian subspecies.

Several hundred spawning *A. triostegus triostegus* were observed in the pass at a depth of about 25 ft. Many of the fish displayed a marked color change. The black bars on the side of the body were much broader (but the added width on either side of each bar was not as intense a black as the center); the median fins were dark, almost black, except for the middle of the caudal which remained pale; the dark median band on the forehead was prominent. Five fish of this color pattern were speared (when pursued, an individual dark-colored manini resumed normal coloration within about 10 sec.); all 5 were ripe males. As many as 4 or 5 of these more melanistic fish were repeatedly observed chasing single fish which were unchanged in color pattern. Two of the normally colored manini were speared. One was a running ripe female and the other a female with opaque eggs which were squeezed from the body only with considerable pressure; thus not all females in the spawning aggregation are capable of reproduction at the same time, which is in keeping with the finding of running ripe female manini in Hawaii along with fish with maturing ova on many different days of the lunar month (Table 6). Actual spawning took place among small groups of fish within the large school which became increasingly active and suddenly darted upward about 8 ft. above the rest. Eggs and sperm were released at the apex of this movement. Swimming was more rapid as the apex was approached. The fish dispersed as they swam back down to mingle with the school. At times two or more small groups joined together in the first few feet of the upward movement, resulting in a dozen or more fish in a compact mass at the top. The attempts to spear individual fish broke up the one large aggregation into several lesser ones in which spawning took place infrequently.

Two other surgeonfishes, *Ctenochaetus striatus* (Quoy and Gaimard) and *Zebrasoma scopas* (Cuvier), were observed to spawn in the Society Islands. Like the manini, they exhibited the sudden upward rush prior to spawning. Possibly the release of eggs and sperm is facilitated by the expansion of the airbladder from the decreasing pressure caused by the upward swimming movement. Like the manini in the pass at Tikahau, both of these surgeonfishes were spawning in a region of strong current to the open sea.

Size and Age at Maturity

The smallest running ripe female seen by me was 101 mm. in standard length. The smallest running ripe male was 97 mm. in standard length. These are probably near the minimum lengths for mature manini around Oahu.

Ten manini were reared in a large concrete tank of the Hawaii Marine Laboratory at Coconut Island from a size of 25 to 27 mm. in standard length beginning on March 17, 1953 (see detailed discussion in section on growth). Two fish of this group, an 89.5 mm. male and a 99 mm. female were killed for gonad study on July 24, 1953. The female had an immature gonad, clear gray in color, and only 5 mm. in length. The ova were minute, only 0.015 to 0.03 mm. in diameter. The male was detected because it was possible to strip a small amount of milt from it, although considerable pressure on the abdomen was necessary. The sperm, however, were not motile. Its testis was slender and 6 mm. long. Subsequent examination of the gonads of the remaining 8 captive manini was not made because of arrested growth of these fish following inadvertent destruction of the algal food supply when seining the tank.

There appears to be considerable variability in the size at maturity. This variability is apparent when the 101 mm. ripe female manini is contrasted with the 127 mm. immature specimen whose egg diameters are graphically illustrated in Figure 8, *C*.

It is doubtful that any female manini spawn during the season in which they first arrived as acronuri in tide pools. Even if the 99 mm. female, which was killed on July 24 following its growth in captivity from a small juvenile on March 17, had been among the first few arrivals to shallow water of the season (middle February), another month of growth and gonad development would hardly seem sufficient to bring a tiny immature ovary such as that seen in this specimen on July 24 to full maturity before the season ended. It also seems unlikely that males will spawn within their first season following recruitment to tide pools.

It seems probable, from a knowledge of growth (see growth section) and the approximate size at maturity, that some manini will spawn in the season following their first sojourn as juveniles in inshore waters. This would be very likely for the first young of the season; the last young of the season would not seem to have sufficient time to develop to sexual maturity before the following spawning season ended. Such a situation would probably increase the variation in the size of the fish at maturity.

Fecundity

Fecundity is defined as the total number of ripe eggs produced by a female in 1 year. It is impossible to ascertain this for fish like the manini which may spawn more than once a year, when the number of spawnings per year is unknown. Therefore only the number of eggs released at one spawning can be determined. This was attempted for only a single manini.

The fish chosen for the egg count was the 123 mm. June 21 specimen, the egg diameters of which are plotted in Figure 8, *I*. This fish had a very large ovary (42 mm. in length) which contained a high percentage of large eggs. These eggs were not completely transparent, and none appeared to have been expelled by the fish. The ovary was vigorously shaken in the vial in which it had been preserved with a minimum of fluid. The agitation released nearly all of the near-ripe eggs from ovarian tissue and placed them in uniform suspension. The contents of the vial were then placed in a graduated cylinder, allowed to settle, and the small amount of excess fluid poured off. A sample of the ovarian mass was drawn off. After its removal, the volume was computed as 26 per cent of the total. All of the large eggs in this sample were counted in successive lots placed in a Petri dish under a binocular dissecting microscope. The sample contained 10,814 large eggs. The total number of large eggs in this ovary was therefore estimated at 40,000.

DEVELOPMENT

Fertilization of the eggs of the manini was effected artificially, using live fish obtained from trap fishermen. As previously discussed, ripe female fish are detected by the release of perfectly transparent eggs following gentle pressure on the abdomen. The milt of running ripe male manini oozes even more readily from the fish than the eggs of ripe females; however, it was found that eggs could be fertilized with sperm from males in which definite squeezing was necessary to bring forth the milt. Eggs were fertilized both by stripping ripe males and females concurrently into sea water with genital apertures in close proximity and by stripping them separately into different containers and subsequently mixing the contents.

The fertilized eggs are spherical, 0.66 to 0.70 mm. in diameter, and contain a single oil globule which is 0.165 mm. in diameter. If suspended in sea water, the eggs slowly rise to the surface. They exhibit no stickiness and do not adhere to objects or one another, although they often lie in single-layered groups at the surface.

Unfertilized (but fertile) eggs are also less dense than sea water. No difference in diameter of unfertilized and fertilized eggs could be detected.

Developing eggs were placed in large finger bowls, an aerated battery jar, and an aerated 20 gal. aquarium. In all of these containers heavy mortality of the larvae ensued because of settling to the bottom (probably through contact with bacteria there and not to any physical injury). Efforts were made to keep the larvae in suspension by placing a fine-mesh false bottom in a battery jar and locating a bubbling aerator stone beneath a hole at one side and by installing a paddle which was slowly turned by an electric motor. Although these methods reduced the amount of settling, mortality was still high and only a few larvae survived to an age of 5 days or more, when oriented swimming began.

In view of the difficulty of rearing larvae in rigid containers, a new approach was tried for the manini. A fine-mesh bag, 1.2 m. on a side, with cork along the top was floated in the Ala Wai Yacht Basin. Fertilized eggs were placed within and allowed to develop. Approximately the same mortality resulted, however.

Once the manini larvae were capable of oriented swimming, they were maintained as easily in unaerated finger bowls as any other way. At this time the critical factor became the supply of food.

The principal stages in early development from 0 hr. to 5 days 22 hr. are shown in Figures 9–12. The drawings of eggs before hatching were made shortly after placing the eggs in 10 per cent acetic acid, a treatment which makes the blastodisc opaque white and the cleavage pattern more visible. The ages given are based on an average development temperature of 24° C. During development the temperature was 24° C. ± about 1°.

Although temperature control was not sufficiently precise to permit an assay of the change of rate of development with changing temperature, it was obvious from the rearing of one batch of eggs at 26° C. ± 1°, that temperature has a marked effect on the rate. The stage attained at 28 hr. 40 min. at 24° C. was reached in about 22 hr. 30 min. at 26° C. The 42-hr. stage at 24° C. was reached in about 32 hr. at 26° C.

No attempt was made to determine the temperature limits within which normal development of the manini is possible. Due to proximity of a light bulb, the temperature of one finger bowl in which 37-hr. larvae were developing was inadvertently raised in a short time to 29.3° C. None of the larvae died at this time.

The blastodisc of the fertilized egg is 0.4 mm. long. One hour after fertilization the first cleavage becomes apparent. At the end of the second hour 8 cells are present, and after 4 hr. about 55 cells can be counted in the blastodisc.

At the age of 6 hr. gastrulation is under way. Epiboly is evident from the thin layer with a wavy edge which is extending downward over the yolk. The cells are very small and are not shown in the drawing of this and subsequent stages.

At 14 hr. the primitive streak is apparent and the cephalic region of the embryo well developed. By about 18 hr. epiboly is complete, and

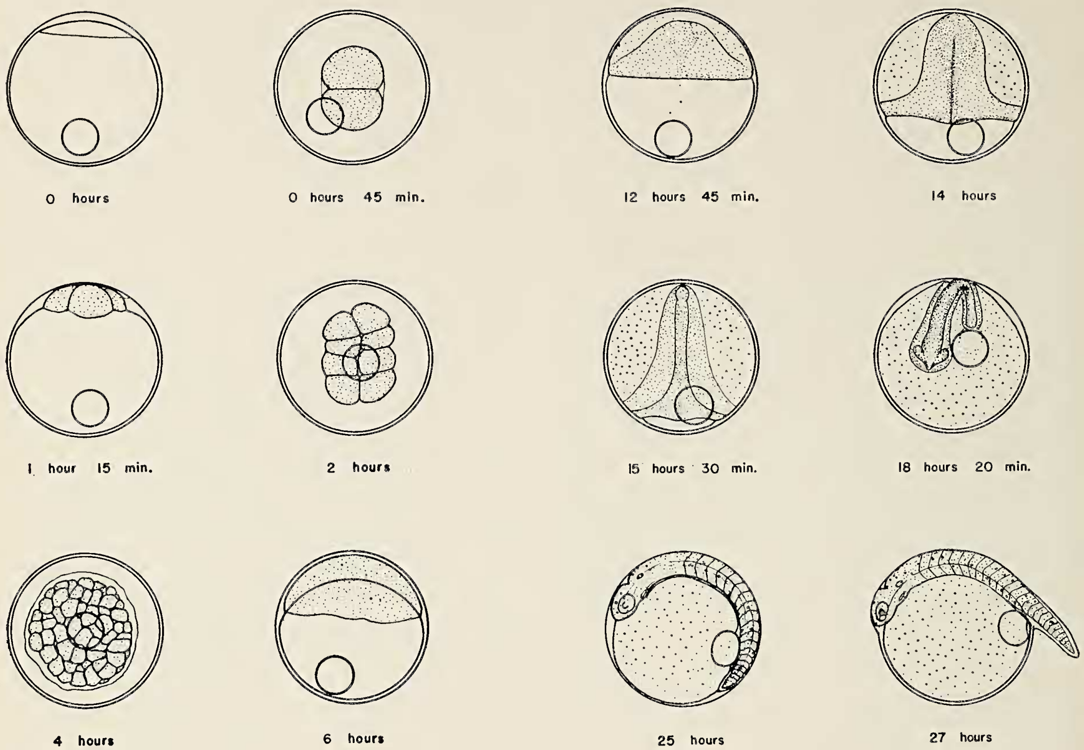


FIG. 9. Developing eggs of *Acanthurus triostegus sandvicensis*. Egg diameter, 0.67 mm.

the yolk plug is visible as a small clear area near the oil globule.

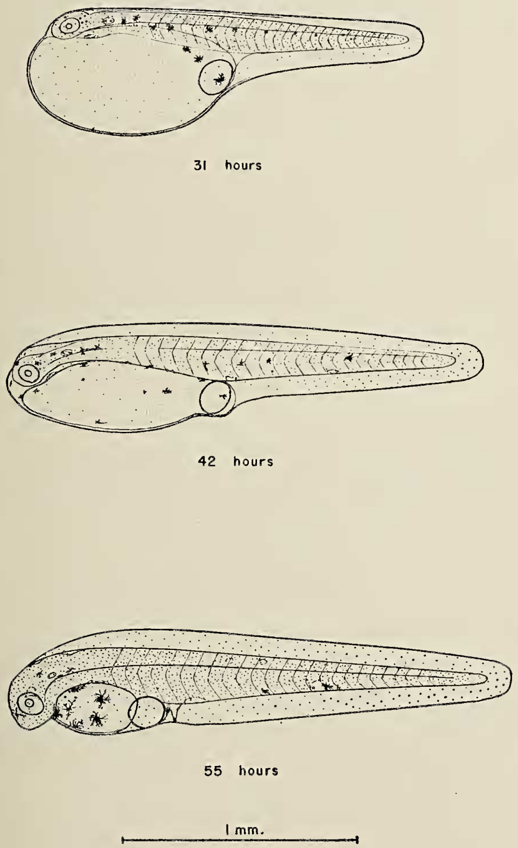
By 15 hr. 30 min. the body of the embryo is beginning to take form and elongate over the yolk. At 18 hr. 20 min. 9 somites can be counted and the optic vesicles are prominent. At 21 hr. 45 min. 12 somites are present. At 25 hr. 19 or 20 somites are visible; the lens of the eye is just starting to form; the auditory vesicle is present and the statoliths are just forming; 24 tiny melanophores can be seen in lateral view on the body; twitching movements are common; the heart contains blood although it has not yet started to beat.

Hatching occurs at the age of about 26 hr. At 27 hr. the larva is nearly 1.7 mm. in length and has 22 somites; the heart is still quiescent. At 31 hr. the heart was observed to beat; occasional short random swimming movements occur by rapid vibration of the posterior half of the body.

At the age of 42 hr. the amount of yolk is reduced to about half of what is present in the 31-hr. larva. As the yolk is used up, the larvae show a progressive tendency to sink. Larvae of 39 hr. still float head down at the surface, but 42.5-hr. fish have begun to settle. The rate of settling of 1 larva at this age was measured at 1.2 cm. per min. The average rate of 3 44.5-hr. larvae was 1.67 cm. per min., and the average rate of 4 47-hr. larvae was 1.88 cm. per min. One 71-hr. larva sank at the rate of 8.2 cm. per min.

At 42.5 hr. some larvae were already settling out at the bottom of the aquarium. Most, however, maintained their level by swimming movements. 300 such movements were observed in an aquarium which contained several hundred larvae. Of these movements, 227 resulted in the larvae being in a higher position in the tank; the rest were sideways or downward. Movements which consisted only of a twitch were not counted. The ability to overcome settling is more efficient than 227 movements with an upward component out of 300 would indicate. Since the head is directed downward, swimming is initiated in this direction. In most cases the fish soon turn sharply and swim upward. If the interval of movement is short, there may be insufficient time to end up higher than the starting position, but usually the fish is not significantly lower. The interval between movements is highly variable, but it averages about 1 min. The distance traveled by the larvae per movement is usually less than 40 mm. One, however, stopped 110 mm. above its starting position.

In addition to geotaxic responses, swimming movements were made to avoid contact with an approaching object. This was first observed in 42-hr. larvae; however, it may be operative several hours earlier. The eyes do not seem sufficiently well developed to be functional at this early age, and a glass rod is detected as easily as an opaque one; thus vision would not seem to be the sense responsible for perception of an approaching object. Before such an object touches a larva, and sometimes when it is as far as 2 or 3 cm. away, a fleeing movement is initiated. A second stimulus soon after the flight reaction will usually result in a second swimming movement. Contact with the bottom due to slow settling usually will not result in a swimming movement. Regular movements occur at about the same rate when the fish are on the bottom. They may enable a larva to become suspended again, but usually only for a short time.


31 hours

42 hours

55 hours

FIG. 10. Early larval stages of *Acanthurus triostegus sandvicensis.*

Areas of white pigment are beginning to form on the ventral part of the seventh and fifteenth somites of the 42-hr. larva. These are large and conspicuous in the 54-hr. larva, and lesser white areas may be seen on the ventral part of the body anterior to the seventh somite and on the head. At this stage the intestine has just formed and the yolk mass is small. The melanophores over the yolk are large and dendritic.

Figure 11 consists of microphotographs of living 75-hr. and 4-day 1-hr. larvae with the light transmitted through the little fish. The dorsal fin fold is a prominent feature at 75 hr. (it was first noticed in the 66-hr. larva), and the pectoral fins are developing. Dark pigment around the eye is evident. The 4-day 1-hr. larva was observed to sink less rapidly than prior stages. One larva of this age sank 2.5 cm. per min. and another less than 1 cm. per min. The 4-day 12-hr. larva remained suspended head down in the water, thus indicating that the air bladder was functional. The jaws were observed to move in the 4-day 5-hr. larva (Fig. 12).

Although still tending to float head downward, the 5-day larva is capable of normal oriented swimming. The pectoral fins can be fluttered rapidly, and the eyes move. The yolk is completely gone and the oil globule half resorbed. By 5 days 12 hr., the 3 individuals which survived to this age appeared to be feeding by short darting movements. Material from a culture of marine ciliates was added to the finger bowl in which these 3 larvae were kept. One

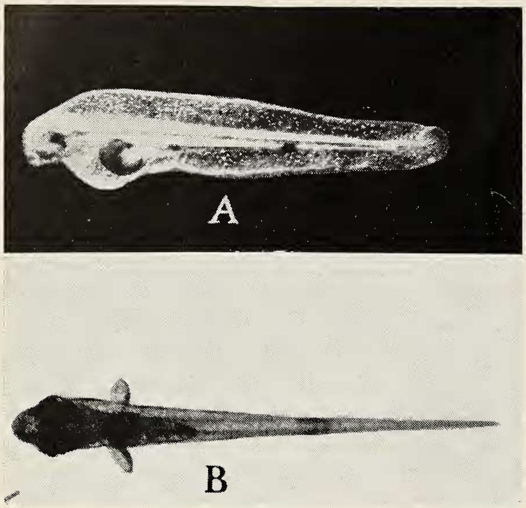


FIG. 11. Microphotographs of larval *Acanthurus triostegus sandvicensis*. *A,* Side view of 75-hr. larva; length 2.3 mm. *B,* Four-day 1-hr. larva in top view; length, 2.5 mm.

died after 5 days 17 hr. of development. Food was present in the intestine of this specimen. The second member of this trio was observed to be dying at the age of 5 days 22 hr. It was removed from the finger bowl for the lower drawing of Figure 12. As may be seen in this drawing, no trace of the oil globule remains, the intestine is convoluted, the liver is prominent, and the gall bladder is visible. The two large white areas on the body have disappeared. The total length is nearly 2.7 mm. The last larva survived to the age of 6 days 12 hr. It grew very little in the last 24 hr., presumably because of insufficient or inadequate food.

Three of the 11 acanthurid lavae from the POFI plankton collections (see p. 216) were identified as manini by dorsal and anal fin-ray counts. They are 6.6–7.0 mm. in total length. Figure 13 is a drawing of the 6.6 mm. specimen (standard length 5.3 mm.). The teeth are not visible without opening the jaws. They are simple canines. The total length of the anterior upper teeth is contained 3.7 times in the diameter of the pupil of the eye.

Specimens smaller than this one could not be identified by ray counts, for the soft rays are not fully formed. A 4.2 mm. specimen could not be positively identified at this time to genus, for only the first three dorsal spines are sufficiently developed to distinguish them from soft rays; however this specimen is about intermediate in structure to the 5-day 22-hr. larva and the 6.6 mm. larva (though is closer to the latter). Its body depth is contained 1.8 times in the total length, and the relative length of the second dorsal, second anal, and pelvic spines is about two-thirds as great as that of the 6.6 mm. larva. The caudal fin is about half formed, the urostyle extending to the posterior part of the incipient fin.

A 4.3 mm. specimen was the only acanthurid found in the POFI larval fish collections which were taken with a 6-ft. modified Isaacs-Kidd trawl, except for an 18 mm. *Zebrasoma veliferum* (Randall, 1955*c*: fig. 3). It was captured near the surface off Kahuku, Oahu. Although a little longer than the specimen just mentioned, it is in a slightly earlier stage of development and is probably a different species. If a large series of specimens were available instead of just a few it might be possible to identify the various stages of the manini to the size where fin-ray counts alone can provide definite identification.

No postlarval specimens of *Acanthurus* greater than 8.7 mm. in length but smaller than the acronurus form were found in any of the POFI collections or museum collections. As previously discussed, specimens larger than about 9 mm.

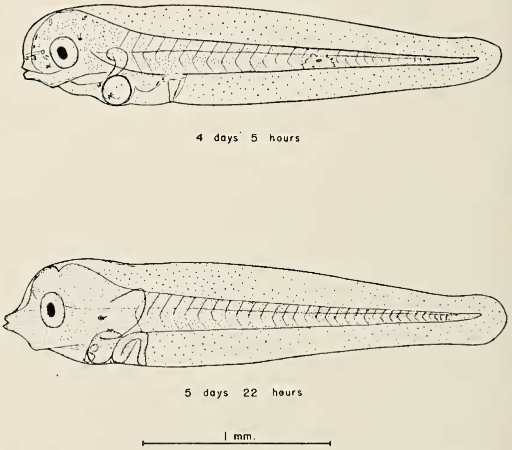


FIG. 12. Larval stages of *Acanthurus triostegus sandvicensis.*

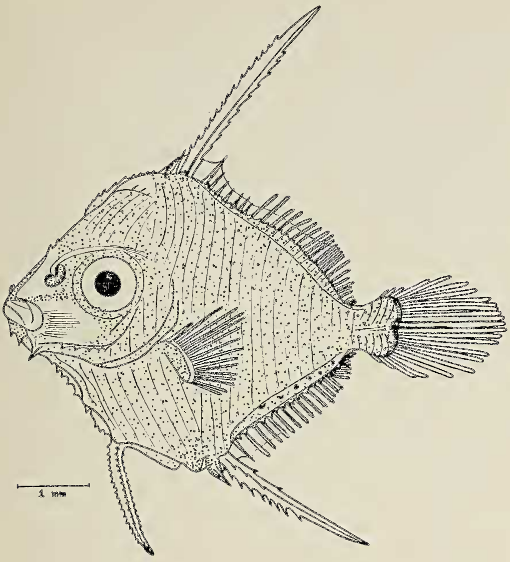


FIG. 13. Postlarval *Acanthurus triostegus sandvicensis* taken in a 1 m. plankton net at a depth of 50 m. at 22° 38′ N., 157° 11′ W.

in length probably elude a meter plankton net. The presence of the 18 mm. *Zebrasoma veliferum* in the collections from the 6-ft. trawl suggests that this would be a better means of catching larger larval acanthurids. The failure to take more acanthurids in the trawl is probably due to the great distance from land of most of the trawl tows.

The only records of the early stages of *Acanthurus* found in the literature are two postlarval *A. coeruleus* identified by Lütken (1880: pl. 5) and an unidentified 7 mm. postlarval *Acanthurus* in Weber (1913: fig. 70). Spartà (1928) reported on a long, ribbon-like, transparent, pelagic egg mass of an unknown teleost fish from the Mediterranean. The early developmental stages which he succeeded in rearing from this egg mass are remarkably similar to those of the manini. Spartà concluded that the eggs were from a species as yet unrecorded from the Mediterranean.

TRANSFORMATION

The late postlarval form of the genus *Acanthurus* is characteristic in morphology, yet identifiable to family Acanthuridae by the presence of the caudal spine and a diagnostic number of fin rays. Originally this stage was placed in a genus by itself, *Acronurus*. The name acronurus has persisted as a common name for this stage, reminiscent of the leptocephalus of eels.

Acronuri are commonly taken at night-light stations. Sixty-two manini acronuri and many of other species collected at night lights and by night-light traps offshore in the vicinity of the Hawaiian, Line, and Phoenix islands were examined. No specimens in night-light collections were found which were smaller than the acronurus stage. It is inferred, therefore, that a positive phototaxis develops in the acronurus. The lack of food material in the gut of night-light specimens (see p. 223) indicates that the presence of numerous small planktonic animals around a light at night is not the attractant. Once transformation to the juvenile stage has begun, the positive phototaxis disappears.

Figure 14 is a photograph of a live specimen of the manini acronurus taken shortly after its arrival in a tide pool. The characteristic transparent scaleless body with silvery abdomen and head (except snout and nape), disk-like form, and vertical striae on the body are apparent. The vertical bars are just beginning to form.

The acronurus comes into inshore regions

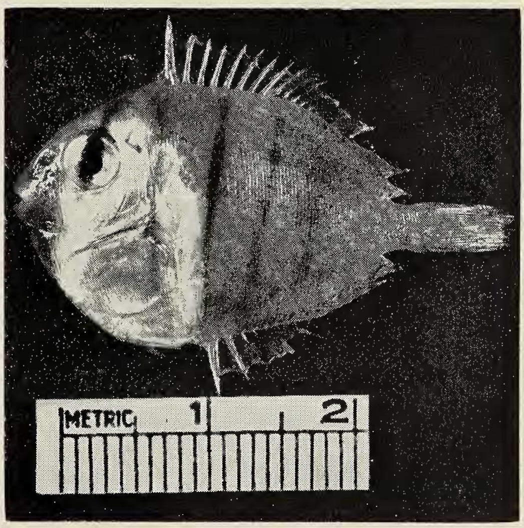


FIG. 14. The acronurus of *Acanthurus triostegus sandvicensis*. Captured at dawn in a tide pool at Diamond Head, Oahu, and photographed alive.

only at night. New arrivals to inshore areas have been collected all through the night, some as early as 9 P.M. and others just before dawn. Most of the night collecting was done at low tide. It is not known whether the influx of acronuri is greater at one phase of the tide than another.

On two occasions before midnight at low tide in ankle-deep water along the shore of the Ala Wai Yacht Basin near the entrance to the Ala Wai Canal, manini acronuri were observed just coming into the area from deeper water. They did not passively float into the shallow zone but swam in rapidly. One crossed several times through the beam of a head lamp before it was caught. If it is assumed that these fish were in deep water beyond the breaker zone before nightfall, then they must have actively swum into the harbor area and not been carried in by any tidal currents. Prior to low tide, tidal currents would be flowing out of the yacht basin and not into it. This is contrary to the belief of Breder (1949*a*: 296) that acronuri of *Acanthurus hepatus* (= *A. chirurgus*) are carried into shallow water by "vagaries of current."

Breder reported observing transforming specimens of *A. chirurgus* at sizes from 23 to 29 mm., and found juveniles from 10 to 20 mm. in length in tide pools at Bimini. He inferred that late postlarval surgeonfish reach a certain size in the plankton at which transformation is possible but continue to grow. The size at transformation is dependent on the size of the acronurus when it reaches shallow water. Breder's explanation of the cause of this variability in transformation size is plausible, although a range of at least 10 to 29 mm. for one species seems high.

From April 11 to October 4, 1953, a total of 175 manini were found in shallow water on Oahu in their first day of transformation to the juvenile stage. Their standard lengths (measured to nearest 0.5 mm.) ranged from 22 to 29.5 mm. Even this would seem, a priori, to be more variation in length than would be expected from mere growth variation alone in the pelagic habitat. A small amount of this variability in Hawaii is due to the change in temperature at which development occurs during the season (Fig. 16 and discussion below), but considerable variation can be seen in the transformation size of acronuri taken within the period of a single month, and therefore cannot be attributed to seasonal temperature differences.

The fluctuation in abundance of incoming young manini has provided an opportunity to test Breder's hypothesis. If the variation in size at transformation were entirely due to normal variation in growth, then no difference should be apparent in the size of manini which are transforming during the time of the month when a big influx is occurring and the period when the recruitment to inshore areas is minimal. If, however, more extremes in size were found when the recruitment is at a minimum, it could be assumed that growth of the manini occurs in the plankton after transformation is possible and that members of a modal group which arrive inshore and transform earlier or later than the majority of the group will be smaller and larger, respectively.

In Figure 15 the lengths of the 116 transforming manini which were collected within the period 5 days before to 5 days after peak tidepool recruitment (taken as 2 days before the time of new moon; see p. 234 and Fig. 6) are compared to the lengths of the remaining manini caught outside this period. Clearly, a higher percentage of extremes in length at transformation occur during the part of the month when the number of acronuri entering shallow water to transform is low.

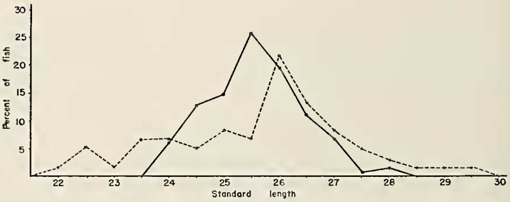


FIG. 15. Size of *Acanthurus triostegus sandvicensis* during the first day of transformation from the acronurus to the juvenile stage. The solid line represents the percent of fish at the designated standard lengths from samples taken 5 days before to 5 days after peak tide pool recruitment (3 days before new moon). The dotted line represents the percent of fish from samples taken during the rest of the lunar month. The solid line is based on a total of 116 fish and the dotted line on 59 fish. Samples include all of the first day transforming manini which were collected from Apr. 11 to Oct. 4, 1953.

If spawning of the manini occurred only during a definite small segment of the month, the dotted curve of Figure 15 would probably be bimodal, one of the modes centered on a low and the other on a high standard length. Since, however, spawning appears to occur throughout the month and merely more prominently in one part than another, most of the young resulting from fertilization at a time of low spawning intensity will come into shoal areas at a more nearly average size during the interval between periods of high tide-pool recruitment and obscure the postulated bimodal effect. The extremes in size of this small group would enter the tide-pool zone at the time of peak recruitment; thus, if the samples were large enough, both curves would extend to the same limits.

The maintenance of populations of manini around small islands such as Johnston Island, the shores of which are constantly swept by a strong current in one direction, would seem to demand some means on the part of the developing pelagic larvae to remain close to land. The presence of small eddy systems around an island might afford the explanation, provided the larvae can stay within such systems. The apparent differentiation of the manini at Johnston Island (Randall, 1956*b*: table 2) and also of *Ctenochaetus strigosus* (Randall, 1955*d*) would seem to rule out the possibility that the Johnston Island populations are derived primarily from fishes which spawn in the Hawaiian Islands proper.

While examining museum specimens of transforming manini from many localities, a definite variation in size with locality was noticed. The standard lengths of the available early transforming museum specimens were measured. These lengths (except those of Hawaiian Islands specimens, already presented graphically) are given in Table 7 with localities and with collection dates when known.

A correlation exists between the size of manini at transformation and the temperature of the water of the locality. The warmest region listed in the table is the East Indies where the mean monthly sea surface temperature may reach 85° F. (29.4° C.) (Hydrographic Office, 225). Here we find the smallest size at transformation, 20–21 mm. Small standard lengths, averaging less than 23.5 mm., are found in other warm areas such as the Palau, Marianas, Gilbert, and Marshall islands (all regions where the mean monthly sea surface temperature exceeds 81° F., or 27.3° C., during the entire year), and southern India in January, and Okinawa in September. Transforming specimens from regions where the temperature is 80° F. (26.6° C.) or less throughout the year or during the month of the date of collection are large, 24 mm. or greater in standard length. These areas include Durban (S. Africa), New South Wales, Ningpo (China), Hawaiian Islands, Mangareva, the Marquesas Islands (in August), and Clarion Island. The large transformation size of the specimens from the Phoenix Islands, where the sea surface temperature exceeds 82° F. (27.8° C.) all year, is an obvious exception to the above. Perhaps the manini population in these islands has differentiated in this respect, although the Phoenix group is not markedly isolated.

In order to preclude the possibility that the different transformation sizes of the different areas are entirely due to genetic factors (reflecting possible races of the manini in all these areas) a comparison was made of the size at transformation of specimens obtained at Oahu in an early cool and a late warm part of the season. Thirty-nine first-day transforming manini were obtained in collections from April 11 to May 8, 1953. The standard lengths of these specimens are plotted as the solid line of Figure 16. The dotted line enclosing the stippled portion of the graph represents the lengths of 38 first-day transforming manini taken from July 7 to October 4, 1953. The average sea surface temperature at Oahu from February to May is 75.7° F. (24.2° C.); the average from July to October is 79.1° F. (26.2° C.), based on average temperatures from 1941 to 1947 presented by Leipper and Anderson (1950). The mean length of the April–May group is 26.256 mm.; the mean length of the July–October group is 25.447 mm. Although the difference in length appears highly significant, a *t* test was made by the group comparison method (Snedecor, 1948: 80). The resulting *t* value of 3.11 gives a probability of nearly 0.001 of obtaining a value greater than this; thus it is extremely unlikely that samples as diverse as the above could be

TABLE 7

SIZE OF *Acanthurus triostegus* AT TRANSFORMATION FROM THE POSTLARVAL TO THE JUVENILE STATE

LOCALITY	DATE	NO. SPECIMENS	STANDARD LENGTH (mm.)	
			Range	Mean
Durban, S. Africa	May 8	2	23–25	24
S. India	Jan. 19	1	22.5	22.5
East Indies				
Sumatra	Dec. 19–25	1	21	21
Moluccas	——	10	19–21	20.2
New South Wales	——	3	24–25	24.3
Palau Is.	Aug. 3–6	7	21–23	22.1
Philippine Is.	Jun.	1	23.5	23.5
Okinawa	Sep. 6–8	2	22	22
S. Japan (30.4° N.)	——	2	21–23	22
Ningpo, China (29.5° N.)	——	5	24–26	24.9
Mariana Is.				
Guam	Jun. 28	3	22–24	22.7
	Jul. 24	7	20.5–23	21.8
	Nov. 25	2	21.5–23	21.25
Saipan	Jul. 9–14	1	22	22
Rota	Nov. 11–13	16	21.5–24	22.5
Marshall Is.				
Bikini	Apr. 1	1	23.5	23.5
	Aug. 17–18	2	22–22.5	22.25
Eniwetok	May 20	2	23–23.5	23.25
Kwajalein	Jun. 24	7	22–24	22.7
	Sep. 1	3	22–24	22
Onotoa, Gilbert Is.	Aug. 21	9	21–25	23.2
Samoa Is.				
Tutuila	Jun. 3	1	22	22
Rose	Jun. 11–14	1	24	24
Swains	May 3–9	1	25	25
Phoenix Is.				
Canton	Apr. 15–28	3	25–26.5	25.8
	May 13	3	25–27	25.8
Enderbury	May 15–19	7	25–27	25.3
Hull	Jul. 7–17	9	23–25.5	24.1
Howland I.	Sep. 24	8	23.5–26	24.3
Line Is.				
Palmyra	Jan. 18	1	23.5	23.5
Fanning	Aug.	1	24	24
Wake I.	Jun. 9	2	23.5–24	23.75
Marcus I.	Aug.	4	25–26.5	25.6
Marquesas Is.	Feb. 3	1	26	26
	Aug.	2	26–26.5	26.25
Makatea, Tuamotus	Feb. 13	3	23.5–25	24.3
	Mar. 15	8	23–25.5	24.4
Mangareva	Feb. 3	7	24–25	24.7
Tahiti	Feb.	1	26.5	26.5
	Apr. 28	1	23	23
	Jun. 16	11	22.5–26	24.2
	Jul. 8	2	23.5–24	23.75
	Aug. 12	4	22.5–24	23.4
	Aug. 28	5	23–25.5	24.4
	Oct. 4	3	25–27	25.7
	Dec. 30	17	22.5–26.5	24.5
Clarion I., Mexico	——	1	25	25

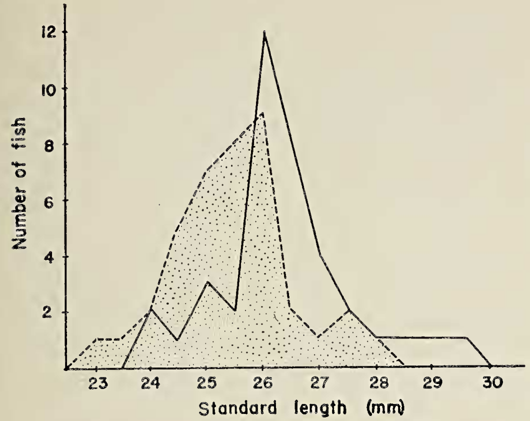


FIG. 16. Size of *Acanthurus triostegus sandvicensis* from Oahu during the first day of transformation from the acronurus to the juvenile stage. The solid line represents all of the specimens collected from Apr. 11 to May 8, 1953; the dotted line indicates those collected from Jul. 7 to Oct. 4, 1953.

drawn by chance from a population in which the transformation length was the same throughout the season. It is therefore concluded that a relationship as indicated above exists between the size of transformation of the manini and the temperature of the water.

Breder (1949*a*) stated that the complete transformation of *Acanthurus chirurgus* occurred in a period of about 48 hr. He did not, however, define the morphological state that constitutes complete transformation. In the manini, adult coloration is nearly acquired after about 48 hr., but other major changes are less than half completed after this length of time. Admittedly it is difficult to define a precise stage at which larval characteristics have completely disappeared and miniature adult structure is assumed. Probably the most convenient criterion is the stage at which the scales have completely formed. Drawings of developing scales have been made by Poey (1875: pl. 3) for the West Indian species, *Acronurus caeruleatus* (= *Acanthurus coeruleus*) and *Acronurus nigriculus* (= *Acanthurus bahianus*). The first evidence of the formation of the scales is the appearance of scattered thornlike outgrowths which project upward as well as posteriorly from the narrow, vertical, fleshy ridges of the body (these spines do not occur on the anterior half of the body). The spines are present on manini acronuri caught offshore at a night light, but they can be seen on these specimens only with the aid of a microscope. They enlarge and become visible (when wet) with the naked eye on the majority of first-day transforming individuals as early as 7:00 A.M. Each such spine on later stages was found to be a central stout ctenius of a single developing scale; the majority of scales, however, do not possess these. As scale development proceeds, the large ctenii flatten and become overlaid with epidermis. When this occurs, scale development is essentially complete as are other major changes of the transformation process. Scale development normally requires 4-5 days. In an aquarium the whole process seems delayed, and about 6 days are necessary.

Figure 17 shows transforming manini on the first, second, third, and fourth to fifth days. The second-day and third-day stages were identified with assurance by comparison with specimens recovered in tide pools following fin clipping on the first day of transformation. No older marked specimens were recovered at the stage when scale structure is just complete, and the time this required had to be inferred from the percentage of specimens in the different stages collected in the weekly poison stations of the Diamond Head tide pool of Figure 4.

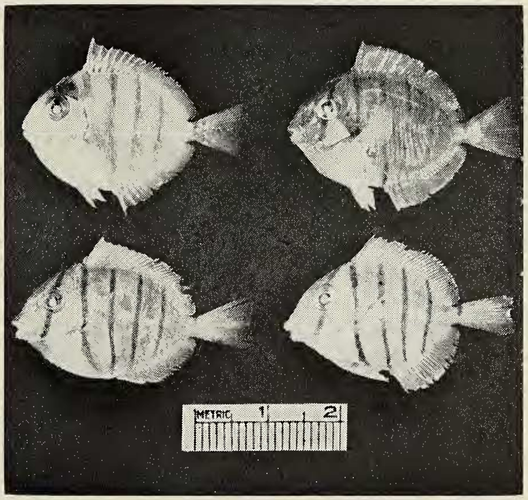


FIG. 17. Transformation of *Acanthurus triostegus sandvicensis* from the acronurus to the juvenile stage. Upper left, first day; upper right, second day; lower left, third day; lower right, fourth or fifth day.

The vertical dark bars which are so characteristic of the manini are absent from the majority of night-light specimens. They are faintly visible on a few such specimens, however. Manini caught in tide pools during the same night when they came in usually possess traces of the dark bars, but some, presumably very recent arrivals, totally lack these markings. One of the two previously mentioned specimens which were observed just entering shallow water from deeper areas of the Ala Wai Yacht Basin had traces of the bars, and the other lacked them. The bars are not dark on any of the specimens collected at night. During daylight of the first day of transformation the bars become intensely dark brown. This suggests that sunlight might accelerate or perhaps even be necessary for the darkening. In a review on the biochemistry of the production of melanin, Lerner and Fitzpatrick (1950: 119) pointed out that ultraviolet irradiation appears to be concerned with melanin formation in at least four different ways, all of which tend to increase pigmentation.

An experiment was designed to determine whether any changes occurred in the transformation process when light is excluded. Two transparent specimens which displayed no evidence of dark vertical bars on the body were taken at midnight. These were placed in a battery jar containing 2½ gal. of aerated fresh sea water. The jar was covered with a box which, in turn, was covered with a heavy black cloth. Three other transparent specimens taken at the same time were placed in a aquarium of about the same capacity which was not darkened. The battery jar was uncovered 12 hr. later. The transformation of the two specimens had barely started. The stage which was reached was about comparable to transforming fish taken shortly after dawn. The bars on the side were barely discernible and the ctenii of the developing scales on the posterior half of the body were just visible. One of the fish was on its side, dying. It was removed, and the jar was again darkened. Eight hours later the second specimen was found nearly dead. The bars were possibly a little darker; the transparency of the body was largely replaced by opaque white, an abnormal color alteration. The three aquarium specimens completed their transformation. The results suggest that light is essential to normal transformation. To be conclusive, however, the experiment should be repeated several times. If light were conclusively demonstrated to be essential to the metamorphosis of the manini, the mechanism by which it exerts its effect would still not be known. It might act directly on the tissues, or by way of the visual sense, or both.

During the first day the transparency of the body is gradually lost. By the end of the day the dark brown bars on one side of the body cannot be seen through the body from the other side as they may be on specimens such as the one in Figure 14. The bright silver color on the abdomen and head is slightly dulled by the end of the day due to the development of melanophores external to the silver layer. The iridocytes causing the silver sheen on the abdomen are present in the peritoneum. On the gill cover they occur in a layer on the underside of the opercular bones. They are found on the surface of the cleithrum at the edge of the gill opening. No silver color is present dorsal to the eye. Instead there is a broad black band which covers the brain. This is found beneath the dorsal bones of the head. By the third day both the silver color and the black band on the head are nearly imperceptible. They are, like the rest of the body except the region of the dark bars, white with numerous, close-set, small flecks of dark brown. The olivaceous cast of the body as seen on juvenile and adult manini is not conspicuous until about the fourth or fifth day of transformation, probably because of slow development of yellow chromatophores.

The second dorsal and second anal spines of the acronurus stage are longer and stouter than the other spines of these fins (Fig. 14). If stuck by either of these spines or by the pelvic spines, a stinging sensation almost comparable in intensity to a bee sting is felt. It is believed that these same spines, very elongate in the 6.6 mm. manini, are venomous in earlier stages. The poisonous nature of the spines appears to be a larval adaptation, for it is lost by the third day of transformation. A diminution in the relative length of the second dorsal and second anal spines may be seen in the series of transforming specimens of Figure 17. The relative change in length of these spines continues until, in late juveniles and adults, the third dorsal and third anal spines are much longer than the second dorsal and second anal spines, respectively. The latter, however, remain thicker. All of the acronurus spines are T-shaped in cross-section; all are solid. The nature of the venom apparatus is unknown. The T-shape of the spines persists into the juvenile stage.

One of the most striking changes during transformation is the alteration of the configuration of the head. This consists primarily of an increase in the length of the snout, resulting in the mouth being in a more ventral position. The rostral prolongation may be seen in Figures 14 and 17. The diameter of the eye (which does not change during transformation) of the transparent specimen of Figure 14 is slightly longer than the length of the snout; in the just transformed manini the eye diameter is contained about 1.5 times in the length of the snout. The osteological changes which accompany the changes in the proportions of the head were not investigated.

A slight increase in standard length occurs during the metamorphosis to juvenile form. After 5 days in an aquarium, three transforming specimens, 24.1–25.0 mm. in standard length, increased 1.2–1.5 mm. in standard length. Most of the increase is attributable to the prolongation of the snout.

A remarkable lengthening of the digestive tract takes place during transformation (Fig. 3). In a period of 4 to 5 days the total length of the alimentary tract of the manini increases about three-fold. This lengthening occurs at the time of a change in food habits from feeding on zooplankton to feeding on algae (see pp. 222–223).

The teeth of the manini acronurus just before transformation are very different from the simple conical teeth of the postlarval manini (as seen in 6.6 to 7.0 mm. specimens). They are close-set and flattened with denticulations on the edges similar to adult teeth. There are about 14 of these teeth, each with 6 or 7 denticulations, in the upper jaw with a broad gap between teeth at the symphysis of the jaw. There are 14 such teeth in the lower jaw with 5 denticulations each. During transformation 8 large adult-type teeth (with about 12 denticulations), which are preformed within the premaxillary bone above the upper series of larval teeth, grow down over the larval teeth which are shed. The more medial of these large teeth are the largest and the first to emerge. In the lower jaw the same process occurs. Six large adult-type teeth with 7 denticulations grow over the larval teeth. Larval teeth lateral to these large ones may persist beyond the period of transformation.

The sequence of tooth replacement is not without variation from specimen to specimen. At the stage when the scales are just completely formed on the body some specimens have fewer than 8 upper and 6 lower teeth in position. Some specimens taken at night lights in deep water appear to be getting their adult teeth prematurely. One specimen of *Acanthurus triostegus triostegus* obtained at a night-light trap at anchorage at Christmas Island already had 6 large upper and 2 large lower teeth.

GROWTH

No information could be found in the literature on growth of any species of surgeonfish. The closest family, phylogenetically, to the Acanthuridae in which growth data are available for comparative purposes is the Teuthididae (Siganidae of most authors). Like the acanthurids, the teuthidids are herbivorous (Suyehiro, 1942; Al-Hussaini, 1947). Whitehouse (1923: 68–70, 83–85) reported that juveniles of *Teuthis java* grew from a length of 25 mm. in April to 75 mm. in September in Silavatturai Lagoon, Tuticorin, India. Ommanney (1949: 48–49) stated that *Siganus corallinus* (= *Teuthis corallinus*) reached a length of 180–220 mm. after 2 years' growth, and about 280 mm. at the end of the third year, in Mauritius.

Information on growth of the manini was obtained by the rearing of fish in a tank of the Hawaii Marine Laboratory, at Coconut Island, Oahu, analysis of the progression of modes among the juveniles of Figure 6, recovery of young fish marked by fin clipping, and the recovery of tagged adults. The data are discussed separately under these headings below.

The standard-length measurement for all of the work on growth of the manini is the length from the tip of the snout to the middle of the

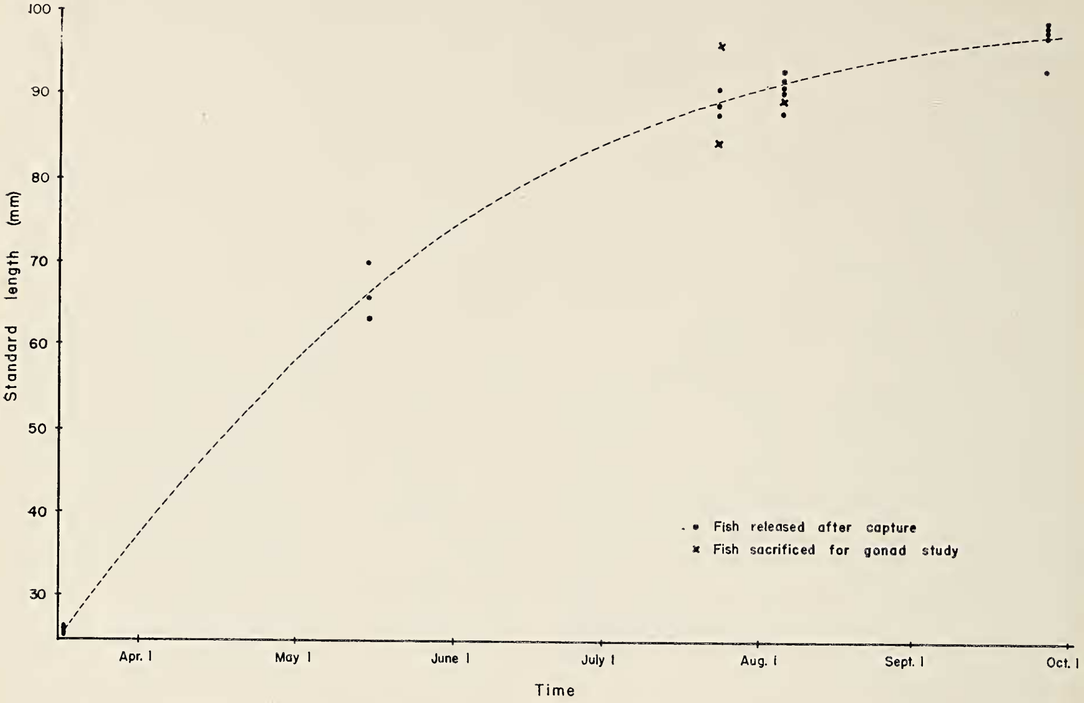


FIG. 18. Growth of *Acanthurus triostegus sandvicensis.* Based on 10 juvenile specimens, 25 to 27 mm. in length, released in a concrete tank at Coconut Island, Oahu, Mar. 17, 1953.

dorsal black bar posteriorly on the caudal peduncle. It was found that this measurement could be made with greater accuracy on living fish than the usual standard length to the base of the caudal fin (i.e., posterior edge of hypural plate). The original measurements are herein retained for all tables, graphs, and discussion (and designated simply "standard length"), rather than converting to true standard length. Should the latter measurement be desired, it may be obtained by increasing the peduncular bar length by 3.5 per cent.

Growth of Captive Fish

Ten manini, 25–27 mm. in standard length (mean length 26.4 mm.), were placed in a concrete tank at Coconut Island on March 17, 1953. The tank measures 34.7 × 10.8 ft. and is an average 3.9 ft. in depth. A constant supply of sea water is pumped into the tank. When the fish were introduced, no other fishes were present and the walls were covered with an exceedingly luxuriant growth of many species of algae. The top of the caudal fin of the 10 juveniles was removed to permanently mark them (see below) as a safeguard against the possible addition of more manini to the tank by other persons.

The growth of these fishes is recorded in Figure 18. The 3 fish captured on May 13 (mean length 66.0 mm.) had grown an average of 20 mm. per month since March 17. On August 6 all of the manini were caught (2 had disappeared and 3 were killed for gonad study). They averaged 90.9 mm. in standard length. By September 27 they had grown to an average standard length of 94.3 mm.; thus the average rate of growth from August 6 to September 27 had diminished to 1.8 mm. per month.

The manini were caught by seining the tank after partially draining it. The efforts to catch them on September 27 failed several times, and much of the algae was detached from the walls of the tank before all of the fish were netted.

Following this the amount of algae on the walls remained slight and apparently insufficient to support the growth of the fish. The 5 remaining manini were measured again on November 19. They were thin, and instead of growing they lost an average of 1.3 mm. in standard length. Manini this size shrink nearly 3 mm. in standard length when preserved in 10 per cent formaldehyde solution.

Growth Measurement from Progression of Modes

The collections of juvenile manini from Kewalo Basin to Makapuu Point, Oahu, plotted in histogram form in Figure 6 permit an estimate of the early growth rate by analysis of the progression in standard length of prominent modal groups from week to week. By this method the growth rate of juvenile manini from about 26 to 45 mm. in length is computed at about 12 mm. per month. Particular reference was made to the mode which first fully appears on the graph on April 17.

Growth of Marked Juveniles

Before undertaking the marking of juvenile manini in the field by fin clipping, experiments were performed in aquaria to test the possibility of fin regeneration. One pelvic fin and the posterior part of the soft portion of the dorsal fin were cut from 3 juvenile manini averaging 27.5 mm. in standard length. Although the fins were severed at the juncture with the body they regenerated rapidly and were nearly completely formed in a month. In a second experiment the top few rays of the caudal fin were cut away as well as the upper corner of the hypural plate to insure the removal of all fin elements. This cutting resulted in the permanent deformation of the caudal fin of the fish.

Ten manini, 28.5 to 30 mm. in standard length (mean 29.25) were caught at the Ala Wai Canal near its entrance to the Ala Wai Yacht Basin on April 24, 1953. The top of the caudal fin of these fish was removed and they were released in the same area. Three of these marked fish were recovered, 1 on May 2 which measured 32.5 mm. in standard length and 2 on May 15 which were 34.8 and 37.0 mm. long (Fig. 19). The average growth rate was 9.6 mm. per month.

Ninety-six juvenile manini, 25–28 mm. in standard length (mean 26.6 mm.), were caught, marked, and released in a Diamond Head tide pool on May 10, 1953. A total of 11 were recovered from this pool on three different dates (Fig. 19). The average growth rate of these fish was 12.9 mm. per month. The 4 manini of this group which were recovered on June 23 ranged from 42.5 mm. to 48 mm. in standard length and averaged 45.1 mm. When first caught with the 92 others on May 10, these fish were a part of the prominent mode which may be seen centered on about 26.5 mm. standard length on the graph for this date in Figure 6. This same mode is still apparent in a sample of 147 fish which were collected at Diamond Head on June 23 in an effort to recover marked fish. At this time the mode is composed of 27 fish, 40 to 49 mm. in standard length with a mean of 43.3. Since the 4 marked manini taken on this date are distributed well within the mode and of larger average size than its mean value, it is concluded that the fin clipping did not retard the growth.

The difference in growth rate between the Diamond Head marked manini and the Ala Wai marked fish may be associated with the difference in algal flora of the two areas. Algal growth in the latter area is sparse; it consists primarily of diatoms. The extraordinary growth rate of the captive manini in the Coconut Island tank is probably also associated with the nature of the algal food supply; the stand of algae was much greater than normally observed in reef or bay areas around Oahu. Invertebrates, including herbivorous types such as echinoids, gastropods, and decapod crustaceans, were present in the tank. It is assumed that the large supply of algae was primarily due to the lack of herbivorous fishes. When introduced to this unusual environment, the 10 juvenile manini were given an unprecedented opportunity for rapid growth.

In view of the more normal environment of the Diamond Head tide-pool region and the similarity in growth rate of marked fish from this region to the rate computed from the progression of modes, 12–13 mm. per month is

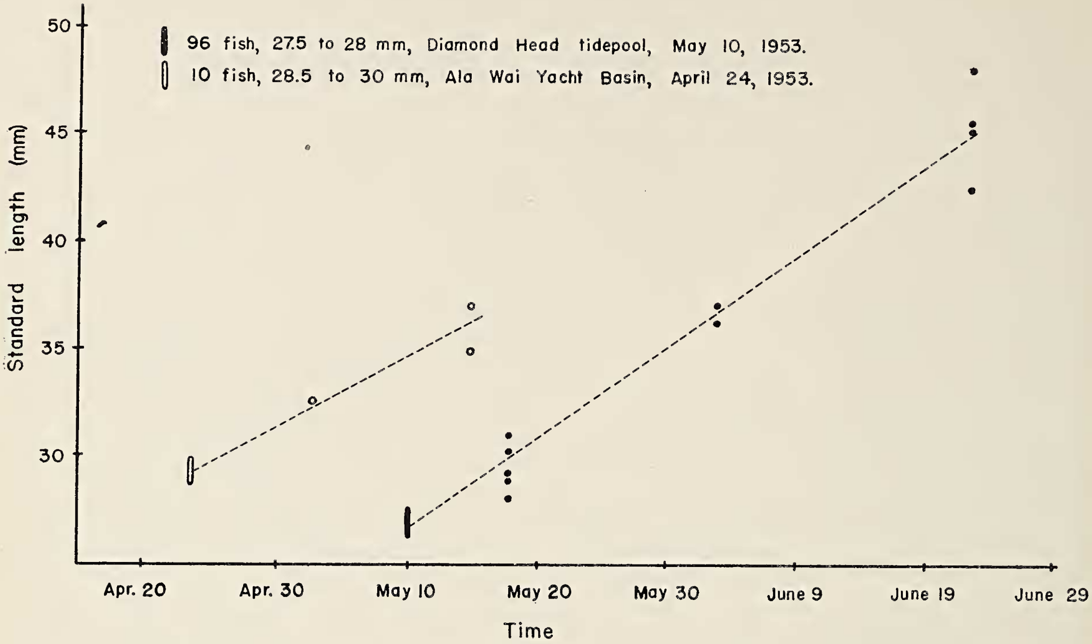


FIG. 19. Growth of juvenile *Acanthurus triostegus sandvicensis* on Oahu. Based on recovery of marked fish.

considered as the probable rate of growth in spring of early juveniles of the bulk of the Oahu manini population.

The growth of juveniles in the winter ceased. This was first noticed from shallow-water collections and observations made during the fall and winter months of 1952–53. Up to November, manini less than 40 mm. could usually be found in the collections or seen in the water. In late November, December, and January no specimens less than 40 mm. were found, but the 40 mm. size persisted. This suggests that the last incoming juveniles of the season, which enter tide pools in early October, grow to a standard length of about 40 mm. by November and then stop growing. During the next two winters the same phenomenon was noted.

In order to demonstrate this cessation of growth and to ascertain the time when growth is resumed, 22 juvenile manini, 40 to 72 mm. long, were caught with a dip net, marked by fin clipping, and released on the nights of January 5 and 6, 1954, at the entrance of the Ala Wai Canal to the Ala Wai Yacht Basin, Oahu. Fish were taken at both the northwest (Waikiki Yacht Club) and southeast shores of the canal entrance. On the two sides of the canal three basic methods of fin clipping were utilized: the top of the caudal fin was removed, the bottom of the fin, and both the top and bottom. Manini of variable size were chosen for each category, and another fin was cut on each specimen. Also any distinctive color marks (usually at the base of the pectoral fin) were noted.

Subsequent efforts to recover the fish were limited by conditions of wind, tide, and turbidity of the water. Although more subject to the effects of turbidity than exposed shores, the Ala Wai area was preferred, for fish are more restricted to the shore area because of the mud bottom away from the bank of the canal. Fish of this size in a region such as Diamond Head move well out on the reef where the broader area, deeper water, and action of surf make them difficult to capture and recapture. Although, as mentioned, some of the larger manini come into tide pools at night, their numbers are not sufficient for such a marking program.

Since fish were measured alive with a light at night, difficulty was experienced in obtaining precise length determinations. Although the lengths were recorded to 0.5 mm., it should be added that variations as great as 1 mm. from the original measurement were noted in unbiased tests of accuracy.

Eleven of the 22 marked fish were recovered; all from the area of release. Two of these were recaptured a second time. Of the 9 fish taken before February 1, few, if any, showed significant growth (Table 8). The 4 recovered on February 21 and 27 displayed a definite increase in size, indicating a resumption of growth during this month in the area tested and for the year 1954.

One other marked fish caught in February and 2 in early March had regenerated the fin other than the caudal fin which had been cut and could not be distinguished from at least 1 other fish of their respective caudal fin categories.

Although there is some indication of a relationship between increasing water temperature and the onset of growth of these manini, the temperature data are inadequate to establish any definite correlation. Temperatures were taken in the canal at night between 9:30 and 12:00 P.M. about 3 in. beneath the surface (Table 9).

It should be emphazied that the temperature at the mouth of the Ala Wai Canal probably varies much more in a day or from day to day than the sea surface temperature off Oahu (mean water temperatures for Honolulu in 1955 are given in Hydrographic Office, 280, as follows: January 24.0; February 23.6; March 24.1). The Ala Wai area is not large and the water is therefore more subject to change due to variation in insolation and atmospheric temperature than the open sea. Probably more important are the changes produced due to variation in the run off of water from Palolo and Manoa valleys which drains to the canal and to the ever variable tides which affect this estuarine region. In order to provide adequate data for the determination of a correlation, temperatures should have been taken at regular intervals each day and an analysis of growth made in terms of average daily water temperatures.

TABLE 9

TEMPERATURE AT THE MOUTH OF THE ALA WAI CANAL

DATE	TEMP. (° C.)
Jan. 5	22.8
Jan. 20	23.2
Feb. 1	23.1
Feb. 27	25.3
Mar. 2	24.7
Mar. 21	24.9

Growth of Tagged Adults

The first tag used on the manini was the Atkins type (Rounsefell and Kask, 1945: 330, fig. 1). It consisted of a single rectangular piece of white cellulose acetate, 5 × 28 mm. in size, and was attached through the back of the fish beneath the posterior part of the dorsal fin with 4-lb. test monofilament nylon. Two small adult

TABLE 8

RECOVERY SIZE OF JUVENILES OF *Acanthurus triostegus sandvicensis* MARKED ON JANUARY 5–6, 1954

STANDARD LENGTH WHEN MARKED (mm.)	STANDARD LENGTH WHEN RECAPTURED				
	Jan. 20	Jan. 26	Feb. 1	Feb. 21	Feb. 27
40.0	41.0				
46.5	47.0				
49.0					54.5
51.5				57.0	
55.0	55.5			60.0	
55.5	55.0				
56.0		56.5			
64.0			64.0		
66.5		66.0			
70.5	70.5				
72.0	72.0			79.0	

manini were tagged and held in a tank at Coconut Island. Within 3 weeks the tags were no longer present on the fish. They were recovered from the bottom of the tank with the loops of nylon intact, thus indicating that the nylon had pulled through the flesh.

The same type of tag was then threaded through the upper part of the hypural plate of the 2 fish. As they swam, the tag of each oscillated slightly as it was drawn along in a position just above the caudal fin. Three months later both tags were in place, and the method looked auspicious. On March 3, 1953, while operating from the fishing vessel "Friendly Isle" owned by Samuel Kaolulo, 50 adult manini were tagged in this manner. Two fish were recovered 5 days later, both in the vicinity of the point of release. No other recoveries were reported. The two Coconut Island manini lost their tags before 6 months elapsed, and further plans for tagging by this method were abandoned. Disappointing results with Atkins tags have been reported by other authors, such as Fraser (1955).

Petersen disk tags were then tried. Since stainless steel seemed most promising among the metals commonly used to attach these tags (Calhoun, Fry, and Hughes, 1951), this material was chosen for initial trials. Considerable difficulty was experienced, however, in bending the free ends of the wire on a struggling fish, a disadvantage clearly pointed out by Calhoun *et al.* Attention was then shifted to nonmetallic substances, of which nylon seemed the most propitious. It is superior to metal in its pliability, nontoxicity, and in not being subject to electrolytic action or fatigue. In order to keep the disks in place, the ends were melted into knobs with a flame (Fig. 20). The position of the tag on the fish is shown in Figure 21. (For a detailed discussion of this tagging method, see Randall, 1956*a*.)

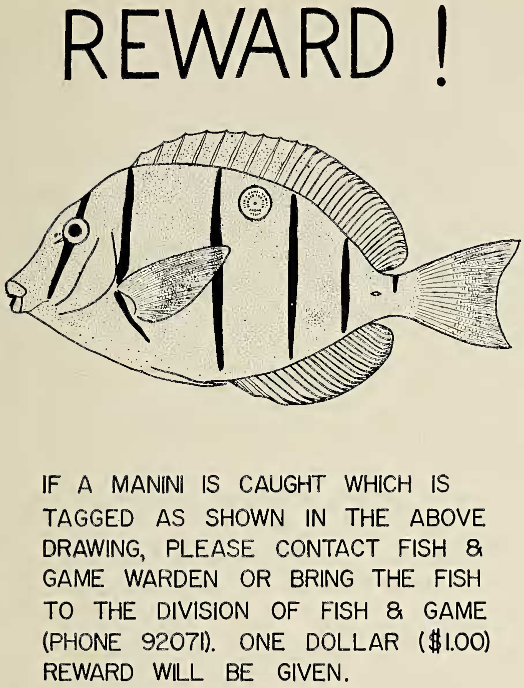
FIG. 20. Petersen disk tag used in tagging *Acanthurus triostegus sandvicensis* on Oahu. The ends of the monofilament nylon connecting the disks have been melted into knobs with a cigarette lighter. The heating caused a blackening of the one knob which is visible.

On August 6, 1953, 3 captive adult manini were tagged with plastic disks by 60-lb. test monofilament nylon (diameter, 1 mm.) and 1 with stainless steel wire.

Seven weeks after tagging, all 4 fish, along with 6 untagged fish which were measured at the time the 4 fish were tagged, were caught and remeasured. The 6 untagged fish, which had a mean standard length of 86.3 mm., had grown an average of 6.6 mm. The 3 tagged with nylon (mean standard length, 84.4 mm.) grew an average of 7.7 mm. The 93 mm. fish whose disks were attached with stainless steel wire added the smallest increment of growth, 2.5 mm. Although there are insufficient data for definite conclusions, it seems apparent that manini tagged with Petersen disk tags fastened with monofilament nylon are capable of normal growth.

One of the fish which survived 11 months until July when the tank was needed for other purposes still retained its disks fastened with nylon. It was noted that the tagging wound was small, and there was no evidence of deterioration of the nylon.

Since the experimental tagging demonstrated no obvious fault in this method, field tagging was begun. Forty-five manini were tagged with hand-made tags. This proved to be most time consuming, and assistance was requested of and granted by the Hawaii Division of Fish and Game. Manufactured tags of laminated cellulose acetate (Fig. 20) were purchased. In order to publicize the tagging, posters (Fig. 21) were



REWARD !

IF A MANINI IS CAUGHT WHICH IS TAGGED AS SHOWN IN THE ABOVE DRAWING, PLEASE CONTACT FISH & GAME WARDEN OR BRING THE FISH TO THE DIVISION OF FISH & GAME (PHONE 92071). ONE DOLLAR ($1.00) REWARD WILL BE GIVEN.

FIG. 21. Poster used to publicize tagging of *Acanthurus triostegus sandvicensis* on Oahu.

distributed by game wardens. Carl M. Nemoto, then working for the Division of Fish and Game, tagged a total of 1,157 manini, 70 to 152 mm. in standard length, from July 6 to November 23, 1954. Forty-five additional fish were tagged on May 4 and June 6, 1955. The tagging was carried out from Kaolulo's vessel between Kewalo Basin and Koko Head, Oahu. The manini were caught in traps, tagged, measured, and released at the place of capture, which was recorded.

Due to the difficulty of using a flame when tagging from a vessel exposed to the strong winds of the Kaiwi Channel (Molokai Channel), Nemoto decided to tag most of the fish by crimping brass leader sleeve on one end of the nylon (the other end was melted into a knob prior to the departure of the vessel). This method was devised by Kenji Ego of the Division of Fish and Game.

Of the total of 1,247 manini tagged with disk tags, there have been 281 recoveries. Of the recovered fish, 173 have been returned alive, providing the opportunity for re-release. Twenty-four of these have been caught again, and 3 have been taken a third time (these recoveries are included in the 281 mentioned above).

The following table shows the lapse of time by 2-week periods between the release and recovery of tagged manini.

The fish with the longest recovery time was tagged on September 21, 1954, and recovered on July 29, 1955.

The explanation of the large number of manini recovered in the first few weeks following release and the sharp drop in returns thereafter probably involves a number of factors, such as mortality, loss of tags, and movement from the immediate area of release.

It is known that at least some loss of tags has occurred, for manini with the tagging wound but without tags have been noticed by fishermen. Since no fish have been seen with a tag in the process of moving up through the back and dorsal fin, it is assumed that most of the early losses, at least, occurred from a dropping off of a disk because of the knob being too small or the brass inadequately crimped. Analysis of the returned tags indicated that the knobs were too small in many cases. When the diameter of the hole in the disk is 1 mm., the knob should measure at least 2 mm.

TABLE 10

RECOVERY TIME OF TAGGED ADULTS OF *Acanthurus triostegus sandvicensis*

WEEKS FOLLOWING RELEASE OF FISH	NO. OF FISH RECOVERED
2	96
4	57
6	42
8	25
10	17
12	9
14	6
16	5
18	4
20	4
22	3
24	5
26	2
28	2
30	2
34	1
40	1

Movement from the trap area could account for a diminution in recoveries of tagged fish; however, evidence is strong against at least extensive migration by this species (see section on migration).

The marked drop in number of recoveries still seems too high to be accounted by any or all of the above reasons. One other possibility exists which is supported by the extraordinary high percentage of early returns. A tagged manini may show a greater predilection to re-enter a trap than untagged manini to enter a first time. This phenomenon has been conclusively demonstrated by Lawrence (1952) for bluegill sunfish in Iowa farm ponds. If such a tendency exists, it might be expected to be greatest in the fish soon after release and gradually abate with time. One manini was caught, tagged, released near the next trap, and caught again in this trap a few minutes later.

The 173 tagged fish which were returned alive were measured alive a second time by Nemoto and released. The remaining tagged manini were measured after they had died, and usually not when fresh but following partial drying and/or freezing. Seventeen of the latter group were recovered within the first 2 weeks following tagging. These fish were all from 1 to 7 mm. shorter than when first measured. The average shrinkage was 3.53 mm. The average standard length of these specimens measured to the peduncular mark is 109.8 mm. The average shrinkage per millimeter of length is therefore 0.032 mm. A correction was made for each fish which was measured dead (unless freshly dead) by multiplying its recovery length by this factor and adding the product to the length.

A total of 70 tagged manini were measured alive a second time following recovery within 2 weeks of tagging. Surprisingly, 46 of these were from 1 to 5 mm. shorter than when first measured; 10 were the same size; 14 were from 1 to 3 mm. larger. The average "growth" was —1.06 mm. A *t* test applied to these data to ascertain the probability of obtaining such a distribution from a population in which no actual change in length occurred resulted in a *t* value of 5.1. With 69 degrees of freedom this gives a probability of less than 0.001 of getting a higher *t* value; thus the null hypothesis of no significant difference is rejected. Since the same person measured the fish both times, the reason for the significantly shorter length is not apt to be any bias in measurement. The shorter length is probably due to shrinkage from starvation in the traps. Manini which are caught in traps may have been held in the traps for a week or more. Although both measurements are made on fish caught in traps, the effects of confinement would be expected to be greater on fish spending another period in traps within 2 weeks of their first.

In order to test the hypothesis that actual shrinkage occurs during starvation, 17 trap-caught adult manini (none showed evidence of long sojourn in traps), 112 to 131 mm. in standard length, were tagged, measured, placed in two large aquaria, and allowed to starve. Eleven days later the 5 fish which survived were remeasured. A definite shrinkage of from 1 to 5 mm. (mean 3.4 mm.) had taken place. The measurements were made by Nemoto.

The large amount of variation (—5 to +3 mm.) in the series of differences between the measurements made on the 70 fish when tagged and recovered within 2 weeks was unexpected. When it is realized that five different sources contribute to this variability, it is more comprehensible. There is the possible error in the first measurement of a living fish. The second measurement of this same fish constitutes an independent source of error. The shrinkage due to starvation is a third. Some manini which are caught have not been in a trap more than a few hours and will not have shortened at all; others held prisoner for a week or more may have shrunk several millimeters. Some manini initially caught after a very short stay in a trap, tagged with a minimum of injury, and recovered a full 2 weeks later after another brief period in a trap might have grown about a millimeter; thus growth itself probably forms a fourth source. An important fifth source of error in the measurement of the dead tagged fish is the variation in shrinkage after death. All of this variability has necessitated a statistical approach to the analysis of the data, and for this purpose the large number of recoveries has been most welcome.

Only those manini recovered after spending

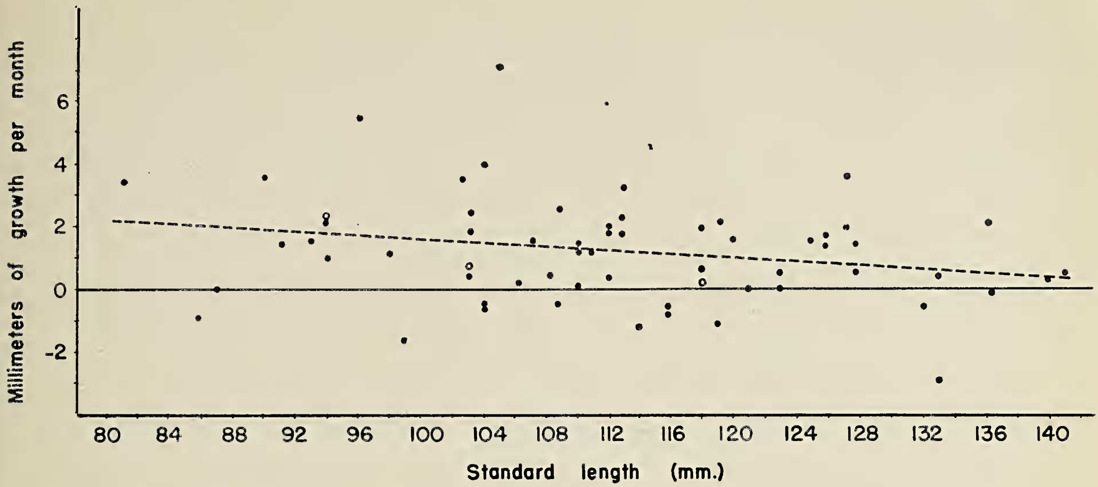


FIG. 22. Growth of *Acanthurus triostegus sandvicensis* on Oahu during the period Jul. 6 to Nov. 19, 1954. The points represent growth increment of tagged fish recovered after at least 1 month in the water. Circles indicate the superposition of one point on another. The dotted line is the regression of growth on standard length.

a month or more in the water following being tagged were utilized for growth study. In Figure 22 the data from 68 such fish, tagged between July 6, 1954, and September 28, 1954, are plotted. The dotted line represents the regression of millimeters of growth per month on standard length. The regression coefficient "b" (slope of the regression line) is —0.0292. The *t* value testing whether this regression differs significantly from zero is 2.085. With 66 degrees of freedom, the probability of getting a larger value of *t* is 0.04; thus the null hypothesis of no significant regression is rejected.

The comparison of the regression line with the upper part of the growth curve of Figure 18 is favorable. The average growth rate of the captive fish from August 6 to September 27 was given as 1.8 mm. per month. The average rate for this size range (90.0 to 94.3 mm.) from the regression line is 1.74 mm. per month.

In order to further confirm the finding of cessation of growth in winter, 155 manini were tagged on November 19 and November 23, 1954, by Nemoto. Twenty-five of these fish were recovered from December 23, 1954, to February 18, 1955 (see Fig. 23). Their average rate of growth is —0.112 mm. It therefore seems likely that no growth occurred during this period.

Tagged manini, recovered after a month or more in the sea, which were at liberty during winter and either fall or spring months have not yet been considered. Data from these fish are presented in Table 11.

If it is assumed that these 22 fish did not grow during any part or all of the 3-month period beginning November 19, and the growth rate of each is computed only from remaining months, an average growth rate of 1.8 mm. per month is obtained. This compares favorably with the rate of growth as indicated in Figure 22 (the average standard length in Table 11 is 110.6 mm.).

AGE

In view of the lack of winter growth of the manini it was hoped that annuli might be detected on the scales; however, none could be seen. Even the circuli of the tiny scales of this species are not very distinct. Cross-sections of vertebrae and otoliths were also examined, but with negative results. It was necessary to grind otoliths to about 1 mm. thickness and view them with subdued light under a compound microscope before any concentric rings could be seen. These were numerous and variable, and none were more sharply defined or grouped closer together than others.

TABLE 11

GROWTH OF *Acanthurus triostegus sandvicensis* RECOVERED AFTER 1 MONTH OR MORE FOLLOWING TAGGING

(Period of tag retention includes both winter and fall or spring months, 1954–55)

DATE RELEASED	DATE OF RECOVERY	STANDARD LENGTH	MEASURED DEAD	GROWTH (mm.)
Jul. 6	Dec. 14	105	×	3.4
23	Mar. 25	110		3.5
30	Dec. 23	115.5		5.5
Aug. 10	Feb. 6	113	×	7.8
10	Feb. 22	110		3.0
13	Jan. 28	98	×	3.1
27	May 17	97		8.0
Sep. 3	Feb. 6	101	×	7.2
3	Mar. 25	102		3.0
21	Jan. 24	98.5		4.0
21	Feb. 18	123	×	7.0
21	Feb. 21	105	×	7.4
21	Jul. 29	101		4.0
28	Dec. 23	121	×	1.8
28	Jan. 21	114		2.0
28	Mar. 25	122	×	1.8
28	Apr. 23	124		1.0
Nov. 19	Mar. 1	105	×	3.8
19	Apr. 5	152		1.5
23	Mar. 19	119		0.5
23	Apr. 27	105		3.0
23	Jul. 6	106.5		7.5

The next approach to obtaining the age of manini was the preparation of the length frequency curve of Figure 24. As the recruitment of the manini is seasonal, it seemed possible that year classes might stand out as modes on such a graph. At least for this curve, however, no definite modes are apparent. Probably the long period of recruitment (February to October), coupled with individual variation in growth, precludes the formation of distinct modal groups in standard length.

Age determinations of the manini would therefore seem possible only by rearing of fish, recovery of tagged fish (tagged at a size small enough to predict the age from growth rate with reasonable accuracy), or gross estimates from growth rate and knowledge of the maximum size.

Although the age attained by the manini is unknown, the following information on the age of two surgeonfishes supplied by Spencer Tinker, director of the Waikiki Aquarium, indicates that at least some acanthurids are long-lived. Two unicorn fish (*Naso unicornis*) which were present in the aquarium when an employee arrived in 1935, lived until they succumbed as the result of an accident in 1955. In 1940 several specimens of *Acanthurus xanthopterus* approximately 5–6 in. in length were placed in the aquarium. Two of these survived until 1951 in a small tank together; they had reached a size of about 20 in. At this time one slashed the

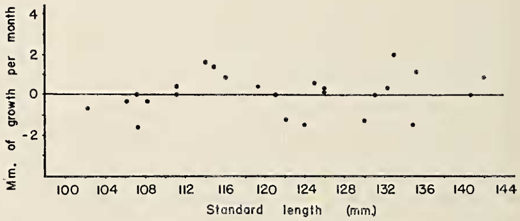


FIG. 23. Growth of *Acanthurus triostegus sandvicensis* on Oahu during the period Nov. 19, 1954, to Feb. 18, 1955, as based on the recovery of tagged fish which were in the water 1 month or more. The horizontal line was added at the zero point to facilitate comparison of the distribution of points with Figure 22.

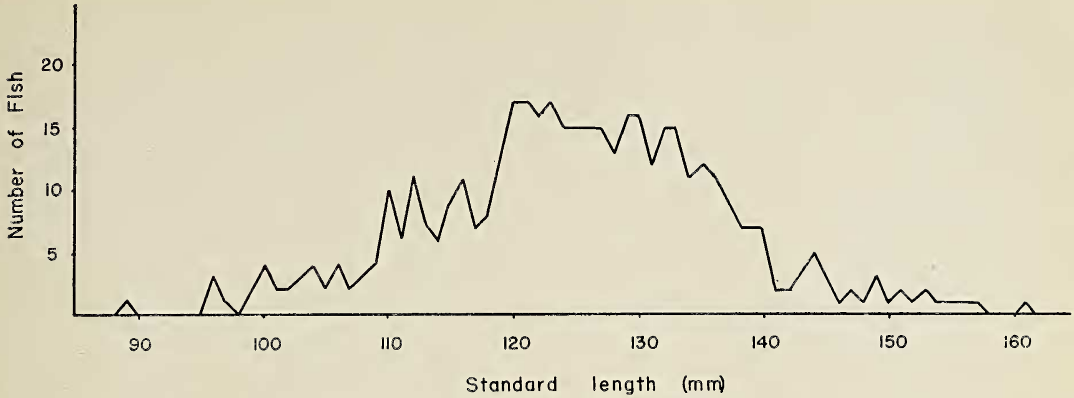


FIG. 24. Length frequency distribution of *Acanthurus triostegus sandvicensis.* Based on 426 specimens caught in traps from Kewalo Basin to Koko Head, Oahu, from Apr. 2 to 9, 1954.

other with its caudal spine and the latter ultimately died. The remaining fish died in 1955 because of an accident.

BEHAVIOR

Migration

Small juvenile manini tend to remain in the tide pool or shallow water area to which they first come from the pelagic state. Some evidence for this has already been presented. Of 176 juveniles taken in the weekly collections during a season from the tide pool of Figure 4, only 19 were 30 mm. or more in standard length and hence definite migrants to the pool from other areas. Since all of the fish in this pool were killed with rotenone each week, a much greater movement to such a large unoccupied area would be expected from the smaller adjacent pools if the species did not exhibit a tendency to remain in one location. When the adjacent pools were sampled for manini, they invariably contained many more specimens 30 mm. or larger, than less than 30 mm. It should be emphasized that these pools are isolated from one another for only about an hour or less during the infrequent low tides less than 0.0 ft. Even in areas like the shore of the Ala Wai Canal and the Ala Wai Yacht Basin where adjacent areas are freely available at all times and essentially identical in cover and food supply, appreciable movement does not take place. This is attested by the success in recovery of marked fish at the mouth of the Ala Wai Canal (Fig. 19, Table 8). Failure to take more of these fish was not due to their movement out of the area but to the difficulty in catching them. Less than one-fourth of the manini sighted were caught, and probably many others were hidden from view under large rocks, etc. None of the fish were taken farther than 20 ft. from the point of release, although the shore was searched as much as 100 ft. away.

On March 7, 1953, a juvenile manini, estimated 36 mm. in standard length, was seen next to the sea wall of the Ala Wai Yacht Basin beside a pier. It was probably among the first manini of the season to come into the area, and was the only individual this size visible for over 100 ft. of sea wall on either side of the pier. On the 9 different days up to March 28 when attempts were made to find this fish, it was seen. Its greatest movement from the place where first observed was only 12 ft. On March 28 it was caught (measured as 41 mm.), and the posterior part of the soft portion of the dorsal fin removed in order to identify it with greater certainty in further observations. It was found on 10 different days up to May 2, but never more than 12 ft. to either side of the pier. On April 24 the dorsal fin had almost completely regenerated and by May 2 the fin appeared normal.

As juvenile manini grow, they migrate seaward from the tide-pool zone (in the harbor area, as mentioned, the larger fish remain in shallow water because of the lack of cover and

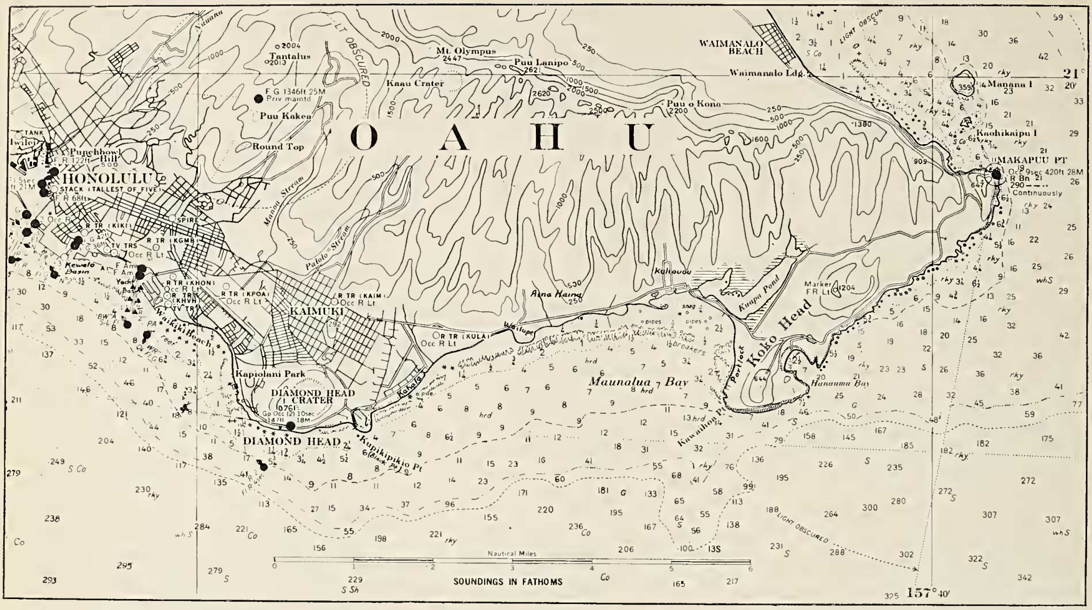


FIG. 25. Southeastern coast of Oahu, Hawaiian Islands (after U. S. Coast and Geodetic Survey Chart No. 4110).

the lack of algae on the mud bottom away from shore). This movement is demonstrated in the graphs of Figure 6. The relative size of any one modal group is progressively smaller in subsequent collections (predation would have to be extremely heavy to achieve the same diminution). The one seeming exception is the large collection of May 29. This, however, was made from a very large pool at Diamond Head which averages about 4 ft. in depth. A higher percentage of larger manini were expected from this collection than previous collections which were all made in pools less than 2 ft. deep.

Information on movements of adult manini was obtained from the recovery of tagged fish. Unfortunately, exact locality data for the areas of release and recovery were usually not available. Since Nemoto was operating from a commercial vessel solely by virtue of the kindness of Kaolulo, he could not delay the fishing to take bearings or soundings. Most locality data from fishermen who recovered tagged manini were also very nonspecific. As a result, little is known of local movements of adults, and only migrations from one major area to the next or the lack of such migrations could be ascertained.

Kaolulo's traps are arranged in groups, most of which are well separated. Nemoto designated these areas as offshore from the following: Yacht Basin, Royal Hawaiian Hotel (Waikiki), Natatorium (near Kapiolani Park), Diamond Head, Black Point, Kahala, KULA antenna, Wailupe, Aina Haina, Kuliouou, Niu Peninsula, Portlock, and Koko Head (Fig. 25).

Of the 281 recoveries of tagged manini 237 were made by Kaolulo; 126 tagged fish, most of which were early recoveries by Kaolulo, were returned to the Division of Fish and Game with no record of where they were caught. This difficulty arose because of his resorting to memory alone to recall the area where tagged fish were taken. When he caught several fish he usually admitted that he could not be sure where any of them were caught. He was finally persuaded to keep record of locality by tag number.

One hundred and thirty-two tagged manini were recovered which exhibited no definite migration. Ignoring fish released in Kewalo Basin for the moment, this leaves only 11 records which indicate that some migration might have occurred. Five of these were fish which were displaced from their home area by movement of the vessel to the next area and which apparently returned to the home area. One was caught at Wailupe, released at Black Point, and caught again at Wailupe. The same fish was not released the second time until the Kuliouou area was entered. It was caught a third time back at Wailupe. Another Wailupe manini was released opposite the KULA antenna and was recovered at Wailupe. Two fish were caught at Black Point, released farther offshore at Kahala, and caught again at Black Point. The remaining 6 records are as follows: 1 fish supposedly migrated from Kuliouou to Wailupe; another went from the KULA antenna to Niu Valley; 2 apparently went from Kuliouou to Wailupe; the last 2 swam from Black Point to Kuliouou. The possibility of error must be kept foremost in mind for all of these apparent migrations. The 2 manini which moved from Black Point to Kuliouou were both caught by Kaolulo on the same day, which seems unusual.

In view of the manner in which the locality data have been reported, it is surprising that more alleged migrations have not taken place. It is therefore concluded that extensive migrations of this surgeonfish probably do not normally occur.

Of the 172 tagged manini which were released a second time 125 were set free on Kewalo Basin. Twelve of these have been recovered. One was taken between piers 7 and 8 in Honolulu Harbor. The rest were all captured either at Kewalo or in the Diamond Head direction. One was taken from a tuna boat in the basin, and 2 off the Kewalo breakwater. One locality reads Ala Moana and another Ala Wai. One manini was caught by Kaolulo with no record of locality. Since his nearest trap is off the Yacht Basin, this fish must have migrated at least this far. One manini released at Kewalo was caught at a depth of 30 ft. directly off the Royal Hawaiian Hotel. A fish from Black Point was caught 6 months later at wading depth off Diamond Head not far from Black Point. The most interesting recoveries of Kewalo-released fish are 2 from Kuliouou which were originally captured at Kuliouou and 1 at Wailupe which was first caught off Wailupe. Although, again, the possibility of error must be kept in mind, it seems unlikely that the only 3 examples of extensive migration (about 8 mi.), all of which occurred among the 12 fish recovered following release at Kewalo Basin, could be mistakes. One of the Kuliouou manini was recorded from this area by tag number by Kaolulo. When questioned of any chance of error, he insisted there could be no mistake. An interval of 3½ months elapsed between its release in Kewalo and its final capture. The other Kuliouou fish was obtained from the Young Market in Honolulu. The interval between the release and capture of this fish was 16 days. The Wailupe fish was recovered by Kaolulo 1 month after release in Kewalo Basin. The locality was reported verbally. The intriguing interpretation of these 3 records of long migration is that at least some manini removed from their home area will continue to wander on the reef until they return. Three records are too few on which to base such a conclusion; therefore more data should be obtained by purposely displacing tagged manini considerable distances from the original area of capture.

Aggregations

Adult manini are often observed in large feeding aggregations which slowly move over the bottom. These groups of fish may be dense and cover areas more than 50 ft. in diameter. What appears to be the same school was repeatedly seen in the same general location at the northwestern end of Manana Island. This group of fish was observed in the area in fall as well as during the breeding season. The behavior of individual manini of the school did not seem to differ from that of solitary adults.

One school of about 300 adult *Acanthurus triostegus triostegus* was observed in the northeast side of the pass at Takaroa, Tuamotu Archipelago, over a period of a week. The school moved as a close-knit mass several feet off the bottom, stopping frequently for periods of several minutes to graze algae. One or two *Aulostomus chinensis* were observed to accompany the school, and the manini were almost constantly harassed by *Acanthurus glaucopareius* which chased individual fish. The school moved as much as 300 yd. in several hours.

Juvenile manini are gregarious and are often seen swimming in groups. One group of 11 individuals, all less than about 36 mm. in standard length, was observed for a period of half an hour at the shore of the Ala Wai Yacht Basin. No fish became separated by more than 12 in. from the rest of the group.

The schooling of *A. triostegus triostegus* during spawning has been discussed previously.

Reaction to Danger

Juvenile manini along the shore of a part of the Ala Wai Canal infrequently visited by man perceive the approach of a person walking along the bank from an average distance of about 20 ft. This distance is contingent on the position of the sun and the depth and turbidity of the water. The usual reaction is a swift darting to some immediate hiding place. If an observer remains immobile, the fish come out of hiding in from about 15 to 25 sec. and resume feeding shortly thereafter. Manini of the same size next to the sea wall of the Ala Wai Yacht Basin, where people pass almost continuously, do not interrupt their feeding at the approach of a person unless some unusual sharp movement is made, at which time they may hide.

The manini in a large tide pool at Diamond Head were observed to have two hiding places, each beneath ledges at the side of the pool. One of these was preferred, and most of the fish swam to it when the pool was approached. When rotenone was spread in the region of this retreat, all of the fish swam rapidly in a direct line to the second ledge, in spite of the turbidity of the water (from the rotenone), even though they had to move in the direction of the observer and pass over a very shallow part of the pool. The part of the pool away from the observer was broader, deeper, free of rotenone at the time, but without good cover. It was evident that the fish were well aware of the location of the best places to seek refuge.

An experiment was designed to determine the time required by juvenile manini to recognize and accept a new site of cover. A small opaque plastic bowl was inverted and placed with one edge elevated from the bottom of a 23 gal. aquarium in which 12 manini, 26 to 39 mm. in standard length, had been kept without a place of shelter for 3 days. Initially this bowl was avoided by all the fish. Fifteen min. elapsed before any fish swam near it. One hr. after the bowl had been added to the tank, the manini were frightened by rapid arm movements all around the aquarium; however none sought refuge in the new shelter. Upon being similarly frightened 3 hr. later, 2 of the smallest fish went into the bowl. Three hr. after this, all of the manini swam to the bowl for cover.

Adult manini are less inclined to seek shelter. Their reaction to an approaching swimmer usually takes the form of retreat. When cover is sought, the hole into which the fish swim usually has two or more entrances. As has been pointed out by Breder (1949*b*: 97) a reaction to attack which alternates between flight and hiding is common among fishes.

Fighting

Juvenile manini may often be seen fighting among themselves in the natural environment. Also, several days after being placed in an aquarium, this behavior becomes noticeable. It increases with time to the extent that it interferes with feeding. After 2 weeks in an aquarium, fully half the diurnal time of 12 juveniles was spent at this activity. The fighting was not associated with territoriality, but took place among all the fish and in all parts of the tank. Three of the larger fish were consistently the aggressors, and the smaller fish usually bore the brunt of their attack, but no definite peck order was established. When only 2 fish were present, however, the larger invariably dominated the smaller and forced it to remain in a corner of the aquarium for much of the day.

A distinct color change, which results in an almost complete reversal of the usual color pattern, accompanies the fighting. The broad pale interspaces between the vertical black bars become very dark, and the upper seven-eighths of the bars change to yellowish white except for a fine dark line in the center of each. On the lower eighth of the body the black bars are faintly visible in their normal width. The more aggressive fish are darker than the less aggressive ones.

The fighting usually involves little actual contact between fish. Most of the time a fish under attack hastily withdraws, a response which generally satisfies the attacker for the moment. When there is no immediate retreat the two fish circle at close quarters and make pugnacious movements, mostly with the posterior part of the body. When a new manini was placed in the tank, it was attacked with ferocity by all of the other manini, but rarely more than one at a time. The hapless fish was pecked over the head and body, strongly bumped, and lashed at with the caudal spines of the others as it scurried from one part of the tank to the next. A manini twice the size of any in the tank was given the same treatment. After about half hour of incessant attack, this oppressed fish was observed to lie on its side on the bottom and submit completely to the relentless abuse. It was caught and examined shortly thereafter. Only a few small scratches on the fins and two small cuts on the body could be seen. The manini has a much smaller caudal spine than other species of *Acanthurus* and is not capable of inflicting much damage with it. Also the jaws do not seem strong enough to injure other fishes of equal size.

Manini were never observed to fight with other species of fishes. They appear to display a dominant behavior pattern to at least some, however. Six small pomacentrids (*Abudefduf abdominalis*) ranging from an estimated 18 to 38 mm. in standard length were observed to intermingle with 4 juvenile manini about 28 to 36 mm. in standard length at the shore of the Ala Wai Yacht Basin. Although the pomacentrids swam close to one another, they usually avoided coming within a body length of any manini. When one did and this was observed by a manini, the latter responded by a slow sideward movement of the body toward the intruding fish. The posterior half of the manini's body was curved toward the pomacentrid and vibrated slightly. The pomacentrid invariably retreated a short distance.

Breder (1948: 293) observed similar behavior in an aquarium with *A. chirurgus*. He noted that a peck order was established among certain fishes in an aquarium. This involved 4 pomacentrids and 1 gerrid. A small specimen of *A. chirurgus* was added which was about equal in size to the largest pomacentrid. Although the surgeonfish was not bothered much by the other fish at first, it seemed to be low or lowest on the peck order. It was never noted to pursue the others, but was occasionally pecked at by the others. Fourteen days later the peck order was modified and the acanthurid was definitely number one. There was little fighting but all kept clear of the surgeonfish which "showed" its peduncular spine to the more timorous.

I have never observed fighting among adult manini. Larger individuals may display dominance over smaller ones, however.

Behavior at Night

At night, both in the natural habitat and in the aquarium, manini rest on the bottom, usually with the pelvic fins and anal fin touching the substratum, in what appears to be a state of torpor or sleep. In general the body color is darker than during the day. Large dark blotches which may be seen faintly during the day between the vertical dark bars are more conspicuous at night. This resting phase is not without movement, for the pectoral fins are almost in constant slow motion and there are vertical undulations of the median fins. When a light was flashed on a darkened aquarium at night, short movements over the bottom were occasionally found to be in progress. These were directed backward more often than forward.

Usually the manini in an aquarium or a tide pool at night are well dispersed. In the normal environment most of the fish choose a sheltered although not a confining location. Many, however, may be seen in very exposed locations. Breder (1948: 294) observed that *A. chirurgus* rested on the bottom of an aquarium at night in the proximity of some shells, but in no case did it enter or hide in the shells.

If light is turned on a sleeping manini at night, and no sharp movements are made, the fish can be lightly touched or even picked up without its making any effort to escape. If a sharp movement is made in the water of the aquarium, or if the fish is roughly handled, it will dart away for a considerable distance over the bottom. This behavior was put to good use for the collection of this species alive. Using a head lamp at night to locate a sleeping fish, a dip net was cautiously placed in front of the quarry. A long stick was used to prod the posterior end of the fish which often responded by swimming into the net.

The following observations on sleep were made on 10 juveniles, 27 to 40 mm. in standard length, which had been maintained in an aquarium for 12 days.

With the onset of darkness the fish settled to the bottom of the tank, although they continued to move about, and occasionally these movements would take them above the bottom. After total darkness ensued, 25 min. were required before they entered the state of suspended animation completely. This state was ascertained by lightly stroking the fish with a glass rod. When they ceased to flee from such contact, it was assumed that they were asleep. Since the period of attaining sleep was prolonged by the interruptions, a series of observations on successive nights was necessary to determine the normal period.

The stimulus to sleep was shown to be the onset of darkness and not merely the passage of a definite number of hours of diurnal existence, for the manini remained active for many hours when a light was kept burning above the tank after darkness set in. In one experiment the fish were kept awake for a period of 24 hr. They remained active during the time; however they ceased to feed toward the end of this period and displayed "restless" swimming.

When the fish were kept in total darkness for 24 hr., they remained relatively quiet on the bottom during the entire period. At the end of this period, however, it was noticed that they perceived the immersion of a hand into the tank regardless of how slowly it was inserted.

After 3 hr. of uninterrupted sleep, beginning with onset of darkness, lights were turned on to see how long the state of torpor would persist. In 13 to 14 min. the first 3 fish awakened and began to swim around the aquarium. These were the largest of the 10 manini. The remaining fish awakened according to size; the 2 smallest required 25 and 28 min., respectively. All of the fish displayed very restless swimming, moving constantly back and forth in the aquarium. When the lights were turned off, they required 39 min. to re-enter the state of torpor. No distinction could be detected in the time needed for the different-size fish to go back to sleep.

SUMMARY

1. In the Hawaiian Islands the common surgeonfish, *Acanthurus triostegus sandvicensis* (known in Polynesia as the manini), is found in many different habitats, although never far from coral or rock for shelter and algae for food. The young are abundant in tide pools.

Manini are not numerous in regions of heavy coral cover, although certain other surgeonfishes are surprisingly common there.

2. The eggs and larvae of the manini are pelagic. Eleven acanthurid larvae, 4.2 to 8.7 mm. in length, were taken in eight plankton tows 10–140 mi. from the nearest Hawaiian island. All were from the upper 50 m., although more tows were made in from 100 to 300 m. A higher percentage of acanthurid postlarvae have been found in surface-caught yellowfin tuna than those taken with long line at depths of about 30 to 160 m. Acanthurid larvae are more commonly found in the stomachs of tuna caught inshore than offshore.

3. The limits of temperature tolerated for 1 hr. by manini (both young and adults) appear to be about 12° and 37° C. Chlorinity tolerance for 24 hr. approximates 1.4 ‰ to 37 ‰. The most extreme readings of temperature found on Oahu in waters inhabited by manini were 16.2° and 35.1° C. and of chlorinity, 2.65 ‰ and 21.3 ‰.

4. Apart from the postlarval acanthurids found in tunas nothing is known of predation on the pelagic stages of the manini. In Hawaii, juvenile manini probably constitute prey to carangid, muraenid, synodid, scorpaenid, sphyraenid, cirrhitid, holocentrid, and antennariid fishes, and possibly certain large crabs. In view of the paucity of large piscivorous fishes in Hawaiian waters adult manini are probably relatively free of predation (man excluded).

5. The manini was found to be parasitized by one species of hydroid, four trematodes, four nematodes, two leeches, and six copepods.

6. Difficulty was experienced at one time maintaining manini in aquaria. They died in

about 48 hr., displaying large sores, eroded fins, and excessive mucus on the body. The dominant bacterium was a short, gram-negative rod.

7. The stomachs of 3 postlarval manini 6.7 to 7 mm. in length were examined for food. Two were empty, and 1 contained two appendicularians and a larval polychaete. Of 57 manini in the acronurus (late postlarval) stage taken by night light offshore, 45 were empty, and the rest contained only occasional fish scales or crustacean fragments lodged in intestinal folds, thus suggesting that the acronuri do not feed at night. The guts of 4 unidentified acronuri taken from a skipjack stomach caught during the day were filled with zooplankton.

8. During the first day of transformation from the acronurus to the juvenile state, most manini do not feed at all. Feeding on algae becomes progressively heavier as transformation continues.

Juvenile and adult manini feed almost entirely on relatively fine filamentous algae of numerous species. Little inorganic sediment was seen in the gut contents. When 28 different kinds of algae plus diatoms were offered to manini in feeding experiments, a red alga (*Polysiphonia* sp.) and a green (*Enteromorpha* sp.) were preferred. All of the blue-greens, the red *Asparagopsis*, and one species of the brown alga *Ectocarpus* were not ingested (although these may be found in stomach contents, mixed with other algae).

9. Juvenile manini were maintained in aquaria on algae alone. Fish 26 to 31 mm. in standard length grew at the rate of about 6 mm. per month (temperature 23.0° to 23.8° C.) when fed either *Polysiphonia* sp. or *Enteromorpha* sp.

10. Manini feed almost constantly during the day, and a large volume of algae is passed through the gut. Four juveniles weighing a total of 8.3 grams consumed 10.8 grams of *Enteromorpha* in 1 day and 8.8 the next. Two adults weighing 83.2 and 94.5 grams ate a total of 27.4 grams of *Enteromorpha* in 1 day. The adult fish did not feed as frequently in aquaria as in the natural environment. The larger fish dominated the smaller one and consumed the major part of the algae.

11. Manini showed no response to extracts of algae, and the visual sense alone is needed to locate algal food. The olfactory sense appears to function in feeding only to avoid unsavory material. Chemoreceptor organs in the mouth and possibly tactile organs as well seem to be associated with the acceptance of algae and the rejection of material not utilized as food.

12. The morphology of the digestive system is briefly discussed. The alimentary tract increases nearly three-fold during the 4 or 5 days of transformation from the acronurus to the juvenile form, reflecting a change in food habits from feeding on zooplankton to feeding on algae. The length of the gut increases from about three times the standard length in small juveniles to nearly six times in large adults.

13. Algae passed through the gut of juvenile manini in 1 hr. 45 min. and in about 2 hr. in adults. At night when feeding ceases, the gut is emptied slowly.

14. Although sustaining growth, the *Enteromorpha* appeared little affected after passing through the gut of manini. Additional work is needed to determine what is utilized by the manini from its algal food.

15. The stomach of the manini varies from slightly acidic to slightly alkaline. The intestine is alkaline (pH 7.7 to 9.1) and the gall bladder acidic (pH 6.2 to 6.4).

Amylase was detected throughout the digestive tract, strongest in the pancreas and weakest in the stomach. The pH optimum of the amylase is about 6.7. Maltase was not found.

Lipase, with a pH optimum of 7.2, was found in all digestive organs, strongest in the pancreas and pyloric caeca and weakest in the stomach.

Proteolytic enzymes are weak, especially from the stomach; pH optimum of pancreatic protease is about 8.4.

16. About two-thirds of the adult manini caught in unbaited traps off Oahu in from 30 to 90 ft. are males. Of 221 manini in museum collections from the tropical Pacific mostly taken from inshore waters, 134 (60.7 per cent) are females.

17. Although ripe males may be taken throughout the year (fewer, however, in the fall), ripe female manini have been found in Hawaii only from early December to late July (and transforming young from middle February to early October). Average monthly sea surface tempera-

tures in the Hawaiian Islands vary from about 75° to 81° F. Enlargement of the gonads appears to coincide with decreasing water temperature in the fall.

18. An estimate of about 2½ months for the duration of larval life of the manini in Hawaii was made by noting the time between the finding of the first ripe females and first transforming young of the season and the last ripe fish and last incoming acronuri.

19. Ripe female manini (*Acanthurus triostegus triostegus*) were found in collections made at islands of the tropical Pacific (where mean sea surface temperatures exceed 80° F. throughout the year) in all months of the year, as were transforming or early juvenile specimens, thus indicating year-round spawning in more equatorial waters.

20. A lunar periodicity in the number of transforming manini was discovered from tidepool collections on Oahu, with the peak in spring occurring a few days before new moon. Since a collection of young from the Gilbert Islands, where water temperatures average about 7° F. higher (and hence development is probably more rapid), indicates peak influx of acronuri approximately at the time of full moon, the periodicity is not attributed to any lunar effect on the young but to greater spawning by adults at one time of the month than another. Thirty-nine ripe female fish were found among 2,552 adult manini examined from 12 days before to 2 days after full moon during the spawning season and 4 among 1,311 fish seen in the remaining half of the lunar month.

21. Individual manini appear to spawn more than once during the season. Large and small ripe females were found near the start and end of the season. No completely spent ovaries were observed until July and August. In graphs of egg diameters of mature ovaries, a mode of egg size about intermediate to the diameter of transparent ripe eggs and primordial ova was invariably present during the season.

No specimens were found with modes of egg size lying between the intermediate-size mode and that of fertilizable eggs, thus suggesting that ripe eggs develop rapidly from the opaque ova of the intermediate group.

22. Although the spawning of manini was never witnessed in the Hawaiian Islands, *A. triostegus triostegus* was observed to spawn in the Tuamotu Archipelago. Several hundred fish were seen in a milling aggregation at dusk during the time of full moon. Many had broader bars on the body and darker fins than normal; 5 of these were speared and proved to be ripe males. Two normally colored manini were females, 1 running ripe. Spawning occurred at the apex of sudden rapid upward movements by small groups of fish. A current carried the eggs to the open sea.

23. The smallest running ripe female manini which was found on Oahu was 101 mm. in standard length; the smallest male, 97 mm. Manini probably do not spawn in their first year.

24. The number of ripe eggs in the ovary of one 123 mm. manini was estimated at 40,000.

25. Early development was studied following artificial fertilization of the eggs. The eggs average 0.67 mm. in diameter, have a single oil globule, and float at the surface. Hatching occurs in 26 hr. at 24° C. As yolk is used up, the larvae show a progressive tendency to sink. They combat this by upward swimming movements. Feeding begins at the age of 5½ days. No young were maintained in aquaria more than 6½ days; however, 3 postlarval manini, 6.6 to 7 mm. in total length, could be identified from plankton collections by fin-ray counts. The most striking feature of their morphology is very elongate second dorsal, second anal, and pelvic spines.

26. Manini acronuri come into shoal water to transform only at night. They are discoid, scaleless, and transparent with a silvery abdomen. Their second dorsal, second anal, and pelvic spines are poisonous. During transformation, which requires 4–5 days, adult-type configuration and coloration is attained, scales form, and the venomous quality of the spines disappears.

27. Light appears to be essential to transformation. Two acronuri taken at midnight were placed in a darkened 2½ gal. battery jar. They failed to transform, whereas 3 others in a comparable but not darkened container completed their metamorphosis to juvenile form.

28. A variation in standard length from 22 to 29.5 mm. was noted in 175 manini acronuri from Oahu in their first day of transformation. One hundred and sixteen were collected in tide

pools from 5 days before to 5 days after peak tide-pool recruitment (2 days before new moon). When the lengths of these manini were compared with the lengths of the 59 acronuri from the rest of the lunar month, a smaller range of length (23.5–28.5 mm.) was apparent for the former group in spite of nearly twice as many specimens. Presumably individual acronuri are capable of transforming some days before the rest of their age group, and hence at a smaller size, when they come inshore earlier than the others. Similarly, those which reach shoal waters later than the majority will have attained larger than average size.

29. A variation in size at transformation was found with locality which appears related to water temperature. The smallest size occurs in the warmest regions (about 20 mm. in the East Indies) and the largest in cooler sectors (Phoenix Islands excepted).

In the Hawaiian Islands the size at transformation averaged 26.3 mm. for 39 specimens collected in April and May and 25.4 mm. for 38 specimens which were taken from July to October (thus developing during warmer months).

30. Growth of juvenile manini, as determined by rearing of captive fish, recovery of fish marked by clipping rays from the top or bottom of the caudal fin, and progression of modes in successive graphs of tide-pool collections on Oahu is about 12 mm. per month.

The recovery of 281 manini of 1,247 tagged with Petersen disk tags fastened with monofilament nylon provided information on the growth of larger fish. The growth of adults 100 to 120 mm. in standard length is slightly greater than 1 mm. per month; 120 to 141 mm. fish grow about 0.8 mm. per month.

Growth of both juveniles and adults ceases during the winter months in the Hawaiian Islands.

31. No annular marks could be detected on the scales, otoliths or vertebrae of manini from which estimates of age could be made. Two larger acanthurids, *Naso unicornis* and *Acanthurus xanthopterus*, lived 20 and 15 years respectively in the Waikiki Aquarium in Honolulu where they died as the result of accidents.

32. Small juvenile manini tend to remain in the tide pool or shallow water area to which they first come as acronuri. With increasing size they move seaward.

Locality data from the recovery of tagged adult manini was too general to determine local movements, but adequate to demonstrate that no extensive migrations are normally undertaken by this surgeonfish. If displaced from their home area, however, manini are capable of wandering distances as great as 8 mi.

33. Manini may be seen as solitary fish, in small groups, or in large feeding aggregations. One large group of fish, although observed to remain in one region in the Tuamotus, moved as much as 300 yd. in several hours.

34. Juvenile manini in a large tide pool on Oahu were observed to have two hiding places beneath ledges, one of which was preferred. In order to attain shelter they will swim toward an intruder, if necessary. From 4 to 7 hr. were required for aquarium fish to accept an inverted bowl tilted on edge as shelter.

Adults are less inclined to seek shelter. Their reaction to an approaching swimmer usually takes the form of retreat.

35. Juvenile manini frequently fight among themselves, both in the natural environment and after being adapted to aquarium life. This does not concern territoriality, but is an expression of dominance by larger fish over smaller fish or old residents (in the case of aquarium fish) over new arrivals. A distinct color change, which involves an almost complete reversal of color pattern, is readily apparent, with the more aggressive fish becoming the darkest. Generally there is no contact between fish, and the fish under attack usually retreat. If not, there is a circling at close quarters with occasional overt movements, especially with the posterior part of the body. The manini's caudal spine is small, and the juveniles were observed to inflict at most only superficial scratches.

Manini were not observed to fight with other species but they may display a dominance in their behavior towards some.

36. With the onset of darkness juvenile and adult manini settle to the bottom, usually with pelvic and anal fins in contact, and enter a state of torpor or sleep. Occasional short movements are made, these more often directed backward than forward. Even when remaining in one place

the pectoral fins are kept in slow motion and there are vertical undulations of the median fins. The color is darker than during the day, and large dark blotches are conspicuous between the vertical black bars on the body. A period of 25 min. after darkness ensued was found to be necessary for the fish to reach a state when they could be lightly touched without fleeing. When lights were kept on in an aquarium for 24 hr., manini remained active, however they ceased to feed toward the end of this period and swam restlessly. A light was turned on after 10 manini, 27 to 40 mm. in standard length, were allowed to sleep for 3 hr. From 13 to 28 min. were required for the fish to awaken, the smallest taking the longest time.

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